Large and small-scale movement patterns of the West Coast rock lobster, *Jasus lalandii.*

Lara Jane Atkinson

Thesis presented for the Degree of Master of Science
in the Department of Zoology, University of Cape Town,
July 2001

Declaration

This thesis documents original research carried out in the Zoology Department, Marine Biology Research Institute at the University of Cape Town. It has not been submitted in whole, or in part for any degree at any other university. Most of the information presented here is original, and all other sources are fully acknowledged and referenced. All assistance I received has been fully acknowledged.

Lara Jane Atkinson

signature removed

16 July 2001

To my parents, Jacqueline and Raymond Atkinson, and my sister Christine: because you always tried to understand.

Table of Contents

Acknowledgements

Before I started this project, I was warned that it was going to be tough, and tough it was. However, with the incredible support and encouragement I received from so many people, it is now complete and I would like to thank my thesis support group. Firstly I would like to thank my supervisors: Prof. George Branch for suggesting this project to me, for always making time and for his continued encouragement, invaluable advise and support throughout; and Dr Steve Mayfield who taught me a lot, was always ready with advice, had an immense amount of faith in me and played a pivotal role in the practical and academic aspects of this project. Thank you both also for the laborious task of editing and greatly improving the manuscript.

As with any project requiring marine fieldwork, there are a large number of people who assisted me over many months with data collection. I am greatly indebted to the core team of people: Paul "*do we have any Tassies?*" Hannekom; Andrew "*cool, I'll do it*" Skowno; Adam "*this is a joll*" West; Steve "*this is divable*" Mayfield; Ronel "*it will be better on the other side*" Nel and Andrea "*I'll be back in a minute*" Plos. Many other people donned their wetsuits and got wet to collect my data and include Henry Gray, Ken Hutchings, Mark Nofke, Cameron Ewart-Smith, Mike De Maine, Bruce Anderson, Rontheo Van Zyl, John and Liz Day, Andrea Pulfrich, Andrew Penny, Craig Smith, Walter Meyer, Peter Fölling and George Du Plessis. Nina Steffani and Barry Clark helped in the field, but their patient assistance with statistical analyses is also greatly appreciated. A special word of thanks goes to Shane Kelly from New Zealand who gave of his time to provide valuable advice in establishing the fieldwork parameters.

Thank you Mike and Linda Tannett for the seemingly endless early morning weather reports and for the wonderful accommodation you arranged for me in Betty's Bay. Thank you to Dr Andy Cockcroft, Dr Johan Groeneveld and Danie Van Zyl from Marine and Coastal Management for allowing me access to the tag-recapture database, for providing logistical support, advice and information. I received a tremendous amount of support and assistance from all the staff at both the Two Oceans Aquarium and the M & CM Research Aquarium, thank you.

I would like to extend a warm thanks to all the staff and students at the Zoology Department of University of Cape Town for helping where they could and listening to my occasional ranting and raving. A special thanks goes again, to Andrea "*I'll be back in a minute*" Plos for the, mostly after-hours technical support, on a wide range of problems, Neville Eden for photographic help and Meg Ledeboer for always being so organized and having both spare keys and money at hand!

The National Research Foundation and the Marine Biology Research Institute financially supported me during this research.

I would finally like to say 'Thank-you very much' to my close friends and family, both near and far, for always trying to understand, offering to help where you could and not completely deserting me when the going got tough ☺.

Abstract

The primary focus of this thesis was to investigate the movement patterns of the South African West Coast rock lobster, *Jasus lalandii*, using a diverse range of techniques. These were (1) an examination of long-term data from an ongoing tag-recapture program, (2) observations on rock lobsters in a mesocosm aquarium, (3) surveys that monitored the seasonal fluxes in activities and abundance of rock lobsters in the field, (4) video recordings of movement behaviour in small aquaria and (5) acoustically tracking the movements of four individual rock lobsters.

On the West Coast of South Africa, large-scale movement (i.e. > 10 km) of *J. lalandii* (> 70 mm carapace length), was examined using a database of tag-recaptures from 1968 to 2000. Only 0.5 % of rock lobsters recaptured over this period had moved more than 10 km, with 0.3 % moving south-eastwards and 0.2 % north-westwards. The data fail to provide evidence for the hypothesized large-scale south-eastward migration of rock lobsters from the West Coast to settle on the South Coast, east of Cape Hangklip.

Rock lobsters were monitored in a mesocosm aquarium that closely resembled the natural habitat of the species, but contained a high density of predatory fish. Shelter fidelity, tendency to aggregate with conspecifics and crepuscular movements were observed under these conditions. The rock lobsters displayed high levels of shelter fidelity, rarely exchanging shelters more than once. They tended to aggregate in the largest shelters available, and there was no indication of crepuscular foraging behaviour. In this environment, they consumed predominantly algae, which were available in or near shelters. The behaviour of rock lobsters in this experiment was considered to be strongly influenced by the intense predation levels in the aquarium.

Monthly observations of rock lobsters in the field in the area east of Cape Hangklip were used to examine seasonal small-scale movement patterns, hole and/or site fidelity, activities and changes in the abundance of lobsters of different size and sex, comparing a marine reserve and a non-reserve area. No fidelity to shelters was evident, nor was site fidelity detected at the scale examined (an area of 1250 m^2). Ovigerous females moved inshore during winter months, but as summer approached and females reached the stage where they would release their larvae, males became more abundant inshore at both the reserve and non-reserve sites. Large rock lobsters (> 80 mm CL) were more abundant at the reserve site compared to the non-reserve site during both the open and closed recreational fishing seasons. The lobsters in this area had relatively low gut-fullness indices and predominantly fed on algae, which reflects the apparent scarcity of more suitable prey items.

The influence of acoustic transmitters on the movements of *J. lalandii* (> 85 mm CL) was tested in laboratory aquaria in the absence of predators. Simultaneously their behaviour was observed near to *vs.* far from shelters. The acoustic transmitters had no effects on the behaviour of the rock lobsters which moved equal distances and at equal speeds whether they carried transmitters or not. Lobsters moved significantly faster when far from shelters, compared to movements near shelters. Unless the lobsters were foraging on food placed far from shelters, most of their time was spent in or near shelters. These behaviour patterns are probably means of minimizing risks associated with exposure.

Acoustic tracking of four rock lobsters for up to 32 days revealed an average rate of movement of 15.5 m/day and a maximum movement of 212 m/day. The furthest distance moved by a rock lobster tracked over 32 days, was 1146 m. The results showed that the acoustic tracking technique has excellent potential for monitoring the movements of *J. lalandii*. Future studies using this technique are strongly recommended and should include extended tracking periods, tracking experimentally displaced rock lobsters and the movements of rock lobsters in response to a red tide.

Chapter 1

General Introduction

This thesis focuses on the movement patterns of the rock lobster, *Jasus lalandii*, and the variety of different approaches used to examine this. Deciphering and classifying the types of movements exhibited by spiny lobsters of the family Palinuridae has been a well-researched topic for almost a century. Although much of their behaviour has been explored, there still remain many unanswered questions. Researchers from around the world struggled to find suitable methods of tracking spiny lobsters for lengthy periods of time. With advances in technology, many species of lobsters have successfully been monitored and their seasonal movement patterns revealed. The first technological advance was the application of sphyrion fish tags to tag large decapods such as lobsters (Scarratt & Elson 1965). These tags were retained after ecdysis, and hence monitoring the movements of lobsters was elevated to a new level. Lobsters could be tagged, released and subsequently recaptured, providing information on their large-scale movements. This monitoring technique greatly enhanced the knowledge gained about the movement patterns of decapods. A second major advancement was the development of acoustic technology, which allowed far more detailed, real-time tracking of the movements of individual lobsters.

Migration is defined as the movement of a population (or a portion thereof) over a considerable distance, either vertically or horizontally, within some confined time period. There may or may not be a return movement and most migrations are periodic with the population moving to a habitat or environmental condition different to that of the place of origin (Herrnkind 1980). Nomadism has been classified as wanderings of an individual over a large area without clear start or end points (Herrnkind 1980). Nomadism is distinguished from migration in that it lacks group directedness, periodicity and temporal confinement (Booth 1997). Homing, on the other hand, is defined as "the periodic, often daily, excursions from a shelter to some nearby area, with subsequent return to that shelter or others nearby" (Herrnkind 1980).

Haakonsen and Anoruo (1994) reviewed the findings of studies on tagging and migration of the American lobster, *Homarus americanus*, on the east coasts of North America and Canada. Ennis (1984a) established that in terms of this species' distributions, "inshore" does not necessarily equate to "shallow water" nor does "offshore" equate to "deep water" alone. Rather, a combination of depth and temperature of water were proposed to be important parameters in

lobster movement and required further examination. Subsequent studies took both depth and temperature into account. The American lobster fishery has traditionally been divided into inshore and offshore stocks with the belief that these stocks do not mix (Estrella & Morrissey 1997). Subsequently, a general consensus was reached that deep-sea *Homarus americanus* make seasonal inshore-offshore migrations and that these long distance movements result in the mixing of different lobster stocks along the coastline (Ennis 1984a; Campbell & Stasko 1986; Campbell 1986; Waddy & Aiken 1992; Estrella & Morrissey 1997). Mature lobsters were shown to move further than immature ones and female lobsters to move further and seasonally earlier than male lobsters (Campbell & Stasko 1986). Coastal populations of *Homarus americanus* were shown to be non-migratory and remain in localized areas within a radius of 3 – 5 km, however a few individuals moved considerable distances (Ennis 1984a; Campbell 1986). Thus, the concept of discrete inshore and offshore lobster stocks has remained speculative (Estrella & Morrissey 1997). Saila and Flowers (1968) first suggested the potential for differences in movement patterns of ovigerous female lobsters. Campbell (1986) monitored the movement of ovigerous lobsters into shallow water (< 20 m) during summer and autumn and offshore into deeper water (> 200 m) during winter and spring. These shallow-deep migrations were suggested to occur to maximize exposure to warmer water temperatures, providing for the completion of egg development. Subsequently, Waddy and Aiken (1992) established that increasing daylength and temperature, associated with the seasonal change from winter into spring, induced ovigerous individuals to spawn. The requirement of warmer water for egg development may induce ovigerous lobsters to migrate further than males to attain sufficient days in warmer waters for egg development to be completed.

Herrnkind (1969) first fully described the mass-migration queuing behaviour of the spiny lobster *Panulirus argus*, which involves diurnal movements of thousands of *P. argus* in single-file queues across sand flats towards an unknown destination. The autumnal mass migration of this species became well-documented and provided important information for its management. Herrnkind (1980) extensively reviewed the movement patterns of most spiny lobsters. Many other species of spiny lobsters were observed to have similar seasonal movements, some onshore-offshore, and others longshore. *Panulirus cygnus* (which occurs on the reefs of Western Australia) displays a seasonal offshore migration in late spring, thought to be predominantly for larval release near strong ocean currents. The ornate rock lobster (*Panulirus ornatus*) also undertakes seasonal migrations to release larvae at the eastern edge of the Gulf of Papua. It is predicted that its larvae are carried back to a different area of the Torres Straight where they settle (Moore & MacFarlane 1984).

The two species of *Palinurus* found on the Eastern coast of Southern Africa, *P. gilchristi* and *P. delagoae,* both undergo migrations (Groeneveld in press; Groeneveld & Branch in press). Long-term tag-recapture data were used to monitor the movements of *P. delagoae.* Individuals spanning commercially captured sizes (55 – 140 mm carapace length (CL)) of both male and female *P. delagoae* were tagged between 1995 and 1997. Forty-eight percent of tagged juveniles (individuals < 65 mm CL) migrated distances greater than 20 km in a north-eastwards direction during the six-year study. These findings suggest that juvenile *P. delagoae* migrate against the prevailing current (contranatent movement) to counter the drift of larvae in the current and thus maintain the location of benthic populations (Groeneveld in press).

A 12-year tag-recapture data set was analysed to investigate *Palinurus gilchristi* migrations. This showed an eastward migration, mostly by juvenile *P. gilchristi* (individuals < 72 mm CL), against the prevailing westward current flow (Groeneveld & Branch in press). The eastern-most populations of *P. gilchristi* showed no migration, whilst the western-most populations displayed the most extensive migration, often in excess of 400 km over three years. Groeneveld and Branch (in press) suggest this eastward migration occurs to redress the downstream displacement of larvae by the westerly current flow. The western populations of *P. gilchristi* migrate to counteract westward larval displacement, whereas the eastern populations appear to use a different larval dispersal and return route that does not require a contranatent migration (Groeneveld & Branch in press).

A review by Booth (1997) summarizes patterns of long distance movement by *Jasus* spp. The studies contributing to this review relied on tag-recapture methods and monitoring changes in commercial catch. *Jasus verreauxi* is found off the shores of northern New Zealand and eastern Australia (Booth 1997) and the two populations are identified as genetically discrete stocks. In New Zealand, Booth (1984) established a clear migratory direction for *J. verreauxi* northwards along the eastern coast of North Island towards the main breeding ground off Cape Reinga. Similar northwards migrations of *J. verreauxi* occur along the eastern Australia coast, but are less defined (Booth 1997). *Jasus edwardsii* (with a similar distribution to that of *J. verreauxi*), contributes substantially to the commercial rock-lobster fisheries in these countries. Long-term tag-recapture studies extending from 1974 until 1982 (Annala 1981; McKoy 1983; Annala & Bycroft 1993) showed that *J. edwardsii* moves long distances (> 5km) on a regular basis. More recent studies by Kelly (1999) have established that *J. edwardsii* displays high site-fidelity and that although individuals may move seasonally to offshore reefs, they often return to the original

shallow reefs. Acoustic tracking showed that females move offshore around the phase of larval release in spring, while males have two peaks of movement offshore, one in summer and one in winter. Offshore aggregations of *J. edwardsii* are commonly found throughout the year, varying in sexual composition with the seasons, reflecting the observed male and female movement patterns (Kelly 1999). Knowledge of the well-defined offshore movements of both *J. verreauxi* and *J. edwardsii* contributes to the successful management of these resources (Annala & Bycroft 1993).

Other *Jasus* spp., such as *J. tristani*, *J. frontalis* and *J. paulensis*, have not been as thoroughly studied in terms of their movement patterns. These species are found near islands or seamounts and sustain only very small fisheries (Pollock 1994; Booth 1997), usually to supply residents living on the islands. There is little evidence suggesting large-scale migration in *J. tristani* and *J. paulensis*, but *J. frontalis* is reported to have a regular offshore migration in spring, returning in late summer (Booth 1997). Booth (1997) suggests that the steeply sloping seafloor, generally associated with islands and seamounts induces a vertical migration, which is as significant as the horizontal migrations displayed by mainland species.

An overall picture of spiny lobster migration has begun to emerge. Many deep-water spiny lobsters undergo long-distance, unidirectional, longshore migration in a direction opposite to the prevailing currents. This is seen as a way of countering displacement of larvae by the currents. In contrast, near-shore species often undertake seasonal onshore-offshore return migrations of shorter distance. The reasons for these are diverse but include release of larvae, avoidance of adverse environmental conditions and reduction of cannabalism.

Herrnkind (1980) classified *Jasus lalandii* as a migrant species. The migratory movements were however, associated only with the incidence of southerly winds and oxygen deficient water being pushed into the rock-lobster grounds. Migration was said to be an adaptation to avoid the effects of low oxygen and the species was otherwise not considered to be a long-distance migrant. Newman and Pollock (1971) found strong evidence for inshore migration of *J. lalandii* during summer months when water with low oxygen-content was reported. Tomalin (1993) and Grobler and Noli-Peard (1997) established that in Namibia, *J. lalandii* migrates seasonally into shallow waters to escape the oxygen-deficient waters offshore. In reviewing the long-distance movements of *Jasus* spp., Booth (1997) suggested that although there was a degree of seasonal inshore-offshore migrations and nomadism, there was no evidence that *J. lalandii* migrated alongshore. All studies thus far classifying *J. lalandii* as a migrant species have been conducted

north of Elands Bay (Fig. 1.1) on the West Coast of South Africa and have been based on the rock lobster's response to oxygen-deficient waters that force them to move inshore (Newman & Pollock 1971; Tomalin 1993; Grobler & Noli-Peard 1997; Booth 1997). Few studies have examined the possible migratory behaviour of *Jasus lalandii* under normal (as opposed to oxygen-deficient) environmental conditions.

Low-oxygen events (anoxia) are defined as oxygen-deficient conditions that occur due to seasonal upwelling and subsequent degradation of organically rich material (Pitcher & Calder 2000). Decay of organic material depletes the oxygen in the water and, in extreme cases, hydrogen sulphide can be produced (Pitcher & Calder 2000). The low-oxygen events are often linked to dinoflagellate blooms, which can sometimes be accompanied by a red colouration in the water, and are often called a red tide. An apparent increase in the occurrence of these algal bloom events has been attributed to the increased nutrient enrichment from land, regional shifts in climate patterns and/or increased introduction of alien species via ballast water (Pitcher 1998). Often associated with red tides are large-scale mortalities of *Jasus lalandii* due to mass "walk-outs" (Cockcroft *et al.* 1998). The most recent of these mass-mortality events occurred in 1997 where an estimated 2000 tons of rock lobster were stranded on the shore. The market loss for this event was estimated to be US$ 50 million (Pitcher 1998). The consequences of these mass strandings for the rock-lobster fishing industry are thus severe.

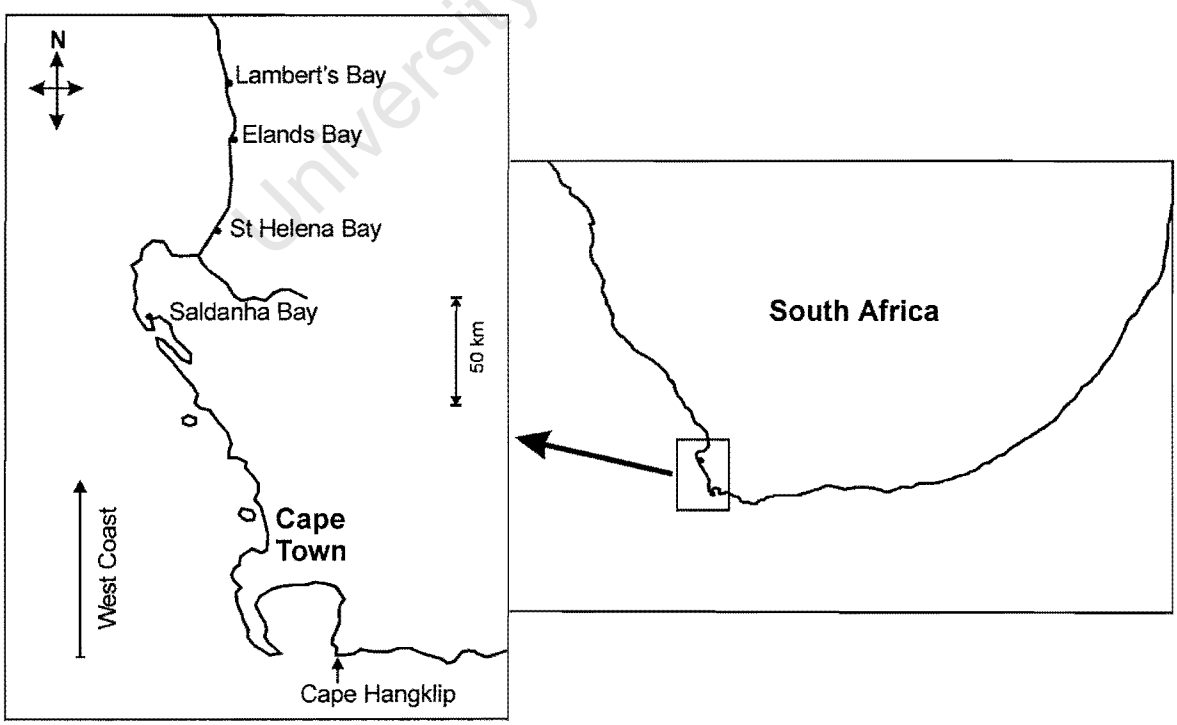

Fig. 1.1: Global positioning of general study area.

In addition to the increasing occurrence of red tide events, there has been a notable decrease in growth rate of *Jasus lalandii* along the West Coast since the late 1980's (Pollock 1982; Pollock & Shannon 1987; Cockcroft & Goosen 1995; Pollock *et al.* 1997). Compounding the decrease in growth rate, shrinkage at moulting became evident in the early 1990s (Cockcroft & Goosen 1995). Shrinkage has been directly attributed to adverse environmental conditions (Cockcroft & Goosen 1995; Pollock *et al.* 1997) possibly caused by the increase in red-tide events. A reduced catch-per-unit-effort has accompanied the decline in rock-lobster yields since the early 1990's (Pollock 1994). A decrease in the total allowable catch (TAC) every year from 1988 to 1996 was a consequence of the declining yields of the species (Pollock *et al.* 1997). Pollock *et al.* (1997) associated the reduced productivity in the southern Benguela with the anomalous *El Niño* years of 1990 to 1993. In combination, these factors were cause for major concern and regulations regarding rock-lobster fishing, both commercial and recreational, were tightened.

Over a time period similar to that of the red tide events and mass mortalities of rock lobsters along the West Coast, Tarr *et al.* (1996) reported a substantial increase of rock-lobster abundance in the South-Western Cape (east of Cape Hangklip, Fig. 1.1). The dramatic increase of rock lobsters in this area was, however, also reason for concern. Rock lobsters (*Jasus lalandii*) prey on sea urchins (*Parechinus angulosus*). These sea urchins provide shelter and protection for juvenile abalone (*Haliotis midae*), which are usually found under the spines of sea urchins (Day & Branch 2000a, Day & Branch in press). The virtual elimination of sea urchins from areas east of Cape Hangklip could have detrimental implications for abalone recruitment in the area (Tarr *et al.* 1996; Day & Branch 2000b). The main abalone fishing region lies precisely in this area, increasing the potential impact of sea urchin declines and associated reduction of juvenile abalone.

Historical records (Heydorn 1969) declare that "*Jasus lalandii* were observed in fair quantities in the Hangklip and Hermanus areas". However, when Field *et al.* (1980) surveyed the area in 1980, *J. lalandii* was so scarce that it was rarely recorded. More recently, claims of substantial increases in rock-lobster abundance east of Cape Hangklip (Tarr *et al.* 1996; Mayfield & Branch 2000), have been supported by increased proportions of recreational rock-lobster landings in the area, the large mean size of rock lobsters caught there, fisher's opinion-surveys and ground-truth sampling. Commercial and subsistence rock-lobster fishing has, until recently, not been allowed east of Cape Hangklip. This may have allowed the rock-lobster population to flourish in the area, provided there was sufficient food source. Forests of the kelp *Ecklonia maxima,* the more frequent habitat of *J. lalandii,* are abundant along this stretch of coastline.

With the obvious increase in rock-lobster densities in the Hangklip and Hermanus areas there has been an understandable increase in demand for access to commercial fishing in the area. Scientists responsible for managing the rock-lobster stock are hesitant to recommend commercial fishing in this area, as it is not entirely understood where these rock lobsters have originated from, if they will remain permanently located in the area, and the extent to which their density increase in this area is part of a delicate ecological balance, involving many species. A holistic approach should be implemented in reviewing the possibility of a commercial fishery east of Cape Hangklip. A closely monitored experimental small-scale commercial fishery is currently in progress in the area with the intention to investigate the effect of commercial catch rates on the population.

Herrnkind (1980) reviewed various approaches used in obtaining data on palinurid movements and concluded that an integrated application of different approaches offers greater potential than any individual technique alone. These methods include monitoring the commercial catch trends, large-scale tag-recapture programs, direct observation via divers or submersibles, ultrasonic telemetry and correlated behavioural studies of captive specimens (Herrnkind 1980). Much broad-scale knowledge of rock lobsters is often gained from monitoring the commercial catch. Advantages of monitoring the commercial catch include a wide geographic coverage, long-term data collection, a large quantity of data and low expense to the researcher (Herrnkind 1980). The same is true for large-scale tag-recapture programs. Disadvantages of these methods of data collection include bias towards areas known to be lucrative fishing grounds and, hence, no sampling of sparsely populated areas, bias against certain individuals of a population induced by trap fishing, and reliance on data that are not independent of the fishery (Herrnkind 1980).

Visual examination by divers of populations provides data on densities, locations and behavioural attributes, with minimal or no disturbance to the animals (Herrnkind 1980). Lobsters are often monitored at this meso-scale level by constraining the study animals in a secluded area or frequently searching a pre-determined area for individuals (MacDiarmid *et al.* 1991). These searches yield data on daily to hourly movement patterns but are often only relevant to animals observed in the particular area and can be difficult to extrapolate to other populations of the same species. Poor weather conditions can negatively influence sampling, yielding reduced sightings and misinterpretation. Another drawback is the limit to the area that can effectively be searched by a diver. Lobsters are highly mobile and can move vast distances, preventing divers from accurately monitoring movements over larger areas.

Technical innovation has introduced a new dimension to monitoring the movements of marine animals, specifically by means of ultrasonic telemetry or acoustic tracking. Remote tracking of rock lobsters allows the rate of movement, the path and the time of movement to be monitored (Herrnkind 1980). Although acoustic tracking offers considerable potential, the equipment is expensive and there are several problems yet to be overcome. The range of transmitter detection is often limited by poor sea conditions, the signal emitted does not allow one to pinpoint the individual's precise location, few (< 10) lobsters can be tracked at a time and ideally tracking should be continuous (Herrnkind 1980). A severe limitation in acoustic tracking is that of the transmitter's battery life. The longer the battery life, the larger the transmitter and the higher potential it has to hinder the animal being tracked. Acoustic tracking does, however, have the benefit of providing real-time data and, with advances in technology, long-term underwater tracking using acoustics may become a reality.

Laboratory studies are often necessary to determine or test isolated effects or responses to specific conditions (Herrnkind 1980). Such is the case when employing any type of tagging system for rock lobsters. The effects of the tag on the animal need to be examined before conclusive results of the natural behaviour of tagged individuals can be obtained (Anderka & Angehrn 1992).

The studies conducted in this thesis made use of all the above-mentioned methods of data collection in examining the movement patterns of *J. lalandii*. Firstly, sphyrion dart tags that are retained after ecdysis were used in a long-term study that relied on data from the commercial fishery to examine longshore movement of *J. lalandii* (Chapter 2). Secondly, external, temporary tags were used to monitor the movement behaviour of rock lobsters in a closed meso-scale aquarium (Chapter 3). Thirdly, observations of externally-tagged rock lobsters were made by divers operating in the field at Betty's Bay, east of Cape Hangklip (Chapter 4). Finally, laboratory tests were conducted to test if acoustic transmitters influence the movements of lobsters (Chapter 5) and acoustic transmitters were then deployed in the field in a pilot study to test their efficiency under field conditions (Chapter 6).

Against this backdrop of previous work on rock-lobster movements and the techniques used to investigate them, a series of ideas and hypotheses were developed and tested in this thesis. The first was whether the decrease in the commercial rock-lobster catch-per-unit-effort on the West Coast of South Africa since the late 1980's could have been due to an eastward migration of

adults, with rock lobsters settling in the area east of Cape Hangklip. This was addressed in Chapter 2, in which long-term tag-release data were used to investigate whether *J. lalandii* undertakes long-shore migrations, and whether these are sufficient in magnitude and frequency to account for the increasing abundance of *J. lalandii* populations east of Cape Hangklip. This study was, of necessity, coarse-grained, relying on data points of release and recapture at approximately annual intervals. To investigate other questions, smaller-scale studies were needed and three different approaches were taken: 1) mesocosm aquarium observations, 2) monitoring of tagged rock lobsters in the field and 3) tracking the movements of individual rock lobsters in the field by means of acoustics. Each approach has advantages and disadvantages as discussed previously.

In Chapter 3, an established mesocosm aquarium was used to test aspects of shelter fidelity, aggregation tendency and levels of crepuscular activity of *J. lalandii* as means of avoiding predators. This contained environment allowed monitoring of an introduced rock-lobster population. Each rock lobster was uniquely tagged, allowing movement profiles to be obtained for individual rock lobsters. This had certain advantages in that rock lobsters could not move out of the study area, poor weather conditions did not impact on sampling frequency or quality and small-scale rock-lobster movements could be observed. However, many factors within the aquarium environment were unnatural, specifically, the high density of predatory fish, leaving the open ocean as the obvious direction of progression.

Monthly field observations of a rock-lobster population in the area east of Cape Hangklip formed the focus of Chapter 4. Antennally tagged rock lobsters were monitored at a site within a marine reserve to investigate hole and/or site fidelity in a total area of 1250 m^2. Population densities of male and female rock lobsters were observed within a marine reserve and compared with an adjacent fished area, in seeking evidence of seasonal onshore-offshore movement patterns, possibly associated with moult cycles. The overall densities and average sizes of rock lobsters between reserve and non-reserve areas were also compared, with the prediction that the reserve would have a higher density and greater average size. Although various movement-related behavioural patterns were explored in this chapter, more definitive, accurate measurements were required and for this, I turned to acoustic tracking.

Before acoustic transmitters were deployed to track the movements of *J. lalandii*, their effects on the rock lobsters were tested in a laboratory environment (Chapter 5). This allowed simultaneous testing of the behaviour of lobsters near to shelters *vs.* far from shelters, in the

absence of predators. Rock lobsters were hypothesised to leave their shelters to forage when food is available but, as a means of risk-avoidance, that their rate of movement would be faster when they were foraging than when they were in the vicinity of shelters. This should lead to rock lobsters spending more time in and around shelters than out foraging.

Once it had been demonstrated that the acoustic transmitters had no effect on the movements of rock lobsters, they were deployed in the field (Chapter 6). This aspect of the work was primarily a pilot study of the utility if the acoustic transmitters, but also to yield qualitative information on the movements of lobsters that allowed me to revisit the results obtained in earlier chapters.

A comprehensive overview is thus obtained using several research approaches and exploring levels of movement on small- and large-scales. The findings, interpretations and implications of this thesis are summarized in Chapter 7, encorporating suggestions for future direction in monitoring *J. lalandii* movement patterns.

Chapter 2

Large-scale movements of *Jasus lalandii* using a long-term tag-recapture database.

2.1 Introduction

The West Coast of Southern Africa has historically been a lucrative fishing ground for West Coast rock lobster, *Jasus lalandii*. Commercial exploitation began in the late nineteenth century and in 1999 was valued at about R150 million (US$ 30 million) per annum (Cockcroft *et al.* 1998). A localized decline in the growth rate of rock lobster occurred in the 1988 fishing season at Elands Bay (Pollock *et al.* 1997). This marked the start of a coast-wide phenomenon of reduced growth rate, which continues to the present day. The cause is unknown, but there have been speculations about it being linked with the *El Niño* phenomenon that is associated with widespread anomalies in weather patterns (Pollock *et al.* 1997). Due to the decreased growth rate, the total allowable catch (TAC) for rock lobster was reduced sequentially each year from 1988 until 1996. During the 1989/90 and 1990/91 fishing seasons, even the lowered TAC could not be filled (Pollock *et al.* 1997). This indicated a substantial decline of rock-lobster yield on the West Coast. Intense fishing compounded the deterioration of the fishery.

Accompanying the *El Niño* years was a reduced frequency and intensity of southerly winds inducing upwelling and an increase in westerly winds (Pollock *et al.* 1997). These conditions encouraged the occurrence of algal blooms, which upon decay, depleted the water of oxygen (Pitcher 1998). This added to the plight of the rock-lobster fishery by causing mass mortalities of rock lobster due to "walkouts" as rock lobsters attempted to evade the low oxygen waters (Cockcroft *et al.* 1998).

Although the collapse in productivity of the rock-lobster resource was associated with the *El Niño* years from 1988 and throughout the early 1990's, the reasons for the collapse are not yet fully understood (Pollock *et al.* 1997). Shrinkage at moulting (Cockcroft & Goosen 1995), decreased yields (Pollock *et al.* 1997) and increasing occurrences of low-oxygen water (Pitcher 1998) all contributed to the concern about the rock-lobster fishery on the West Coast. With the decrease in adult rock-lobster spawning stock on the West Coast there would almost certainly have been a concomitant decrease in larvae released from this area.

During the early 1990's a notable increase in rock-lobster abundance occurred in the South-Western Cape region (Tarr *et al.* 1996; Mayfield & Branch 2000). The increase in this area was intuitively coupled with the decrease on the West Coast and it was predicted that an eastward migration had occurred. There was, however, little substantive evidence to support the idea of an eastward migration and this theory has remained speculative.

The larvae of decapod crustaceans are widely dispersed via ocean currents, and the time period spent in this dispersal phase differs between species. The phyllosoma larvae of *Jasus lalandii* undergo 11 moult cycles during the dispersal phase, settling after 7 to 8 months (Silberbauer 1971). Few studies have investigated larval occurrence in oceanic waters, but Booth and Ovenden (2000) sampled across approximately 16 000 km of ocean in a search for the larvae of *Jasus* species. Larvae were only found near to areas of adult populations. Booth and Ovenden (2000) suggested that larvae use behavioural strategies or physical mechanisms to prevent being carried too far from adult grounds. The exact route taken by any species of phyllosoma larvae has yet to be defined, but the maintenance of allopatric populations of different species strongly suggests larvae have well developed site-selection mechanisms. Ocean currents and flows distribute larvae. Variable pueruli settlement rates have been linked with anomalies in current flow (Caputi *et al.* 1996; Phillips & Pearce 1997). The South Atlantic gyral circulation greatly influences the dispersal of several *Jasus* spp. (Cobb 1997). The weather anomalies linked to the *El Niño* years caused anomalies in ocean currents as well. These may have altered the settlement of larvae in certain areas. The practical difficulties in tracking phyllosoma larvae eliminates the possibility of accurately establishing if the increase in the rock-lobster population in the South-Western Cape was due to increased larval settlement in this area.

Marine Protected Areas (MPAs) are areas where all forms of fishing and extractive use are banned (Childress 1997). The limitations imposed by MPAs are designed to create zones within the coastal shelf where an undisturbed habitat exists for comparisons with areas where human impact has modified the ecosystem (Childress 1997; Babcock *et al.* 1999; Kelly *et al.* 2000). Among many other functions, Marine Protected Areas serve as a source of larval supply, with the potential for larval settlement both in and outside the MPA. MacDiarmid and Breen (1992) reported that either puerulus settlement or juvenile survival (or both) were higher in the marine reserves they examined. It however, remains to be resolved whether the presence of adults provides cues for larvae promoting their settlement in the area. Besides the obvious protection offered to adult stocks by MPAs, they also potentially increase the numbers of rock lobsters moving out of the reserve into fishing grounds (the spillover effect) (Childress 1997). Kelly *et al.* (2000) suggest that with an

increasing population within reserves, food or suitable habitat may become a limiting factor. Mobile species might thus emigrate to unprotected areas and in this way become available for capture. The boundaries of marine reserves are often perceived to be lucrative fishing areas. The commercial catch rates near the Leigh Marine Reserve in New Zealand support this perception in that they "are relatively high compared with areas remote from the reserve" (Kelly 1999).

The current Marine Protected Areas around the Western Cape province of South Africa include three rock-lobster sanctuaries and five smaller marine reserves where all forms of life are protected. The effectiveness of these conservation areas are presently under review (Mayfield *et al.* in press) and the current draft proposals for new Marine Protected Areas will enhance the protection of valuable rock-lobster stocks.

This chapter examines tag-recapture data provided by Marine and Coastal Management, South Africa, spanning 1968 until 2000, and one year of tag-recapture data provided by the Namibian Ministry of Fisheries and Marine Research. Although the data were originally collected specifically to monitor the growth rate of *Jasus lalandii*, they are also suitable for detection of large-scale movements. The data cover the major period of commercial exploitation, including the early lucrative harvesting phase, when anecdotal reports of mass migrations of *J. lalandii* were common, through to the current situation with much reduced stocks. Mayfield and Branch (2000) have shown that in recent years there have been dramatic increases in rock lobsters in an area east of Cape Hangklip (in the South-Western Cape, see Chapter 1, Fig. 1.1 for locality). The hypothesis tested was that the decrease of catch-per-unit-effort on the West Coast was as a result of migration around the coast, with rock lobsters settling east of Cape Hangklip

2.2 Methods

All available tag, release and recapture data for the period 1968/69 to 1999/2000, were obtained from Marine and Coastal Management (M & CM) in unprocessed format. They were originally collected for an ongoing study of the growth rate of *Jasus lalandii* but have not previously been used to explore movement patterns. Goosen and Cockcroft (1995) provide a detailed methodology for the tagging procedure, but a brief description follows.

Rock lobsters were captured annually between July and October by trap or hoopnet from either research or commercial fishing vessels. Male rock lobsters larger than 75 mm carapace length (CL) were tagged with either a FT 2 dart tag inserted between the second and third abdominal segments

or with a FD 68B sphyrion tag between the carapace and the abdomen (Goosen & Cockcroft 1995). Some female rock lobsters larger than 70 mm CL were tagged in a similar manner between 1968 and 1980. The rock lobsters were then released at the site of capture. Data collected at the time of tagging include the area of capture, the area and date of release, the rock-lobster carapace length (CL), moult stage and the number, if any, of missing appendages. A coast-wide tag-return incentive scheme was introduced to encourage fishers to return tagged rock lobsters and all information relating to the catch. All recovered rock lobsters were re-measured and the area and date of recapture noted. Tagging in the area east of Cape Hangklip only began in the late 1990's and is reported separately from the other data.

The Ministry of Fisheries and Marine Resources (MFMR) of Namibia has conducted small-scale rock-lobster tagging operations between 1985 and 1988, similar to those conducted by M & CM described above. However, only the tagging data from the 1986/87 fishing season could be provided by MFMR.

All rock lobsters that were recaptured at a site different to that of release were separated out. For each of these rock lobsters, the distance between the midpoint of release area and the midpoint of recovery area was measured using a nautical chart. The fishery for the West Coast rock lobster is divided into fishing zones and the information relating to the release and recapture sites is only accurate to within the limits of these zones. No global positioning system (GPS) positions are available, hence the midpoint measure was the best approach to estimate the distance moved. The distance was converted from nautical miles to kilometers. If a rock lobster was found to have shifted 10 km or more, it was considered to have moved. The general movement direction (north, south, east or west) was determined and the total number of days-at-large calculated. The estimations of distances moved by rock lobsters were the shortest possible distances between release and recapture sites, although this must be an underestimation of the total distance travelled, as movement seldom occurs in a straight line. There may have been occasional errors in recording the precise location of release and recapture sites, and in recording tag numbers. The data are thus interpreted with caution.

All rock-lobster movement-data were processed as follows: First, the number of tags returned between 1968/69 and 1999/2000 for each area were summed (x) and the total number of rock lobsters with tags moving out of that area (y) was subtracted from the value x (equation 1). These values were converted to percentages (equations 2 and 3) and square root transformed for presentation of the data. These transformed data are presented as circles, the diameters of which

are proportional to the transformed percentages of rock lobsters remaining in the area of release, or moving to other areas.

Number of lobsters not moving ..... $t = x - y$..... (equation 1)
% lobsters not moving..... $t\% = t/x * 100$ ..... (equation 2)
% lobsters moving out of release area ..... $y\% = y/x * 100$..... (equation 3)

2.3 Results

The average recovery rate of tagged lobsters was 15.7 % per season. Of 32 fishing seasons, large-scale rock-lobster movements were detected in only 10 (Table 2.1). Of 43 675 rock lobsters recaptured over the whole period, a total of 73 moved northwards and 139 southwards. Thus 0.5 % of the recaptured rock lobsters were detected to have moved 10 km or more. The deduced movements of rock lobsters are represented in Fig.2.1. The average distance moved was 49 km and the average time spent at large was 350 days (Table 2.1). All rock lobsters that were detected to have moved were sexually mature males. The average time spent at large of those recaptured rock lobsters that were not recorded to have moved was 264 days. The movements of two individual rock lobsters from PN4 to CP1 are not represented in these figures as they spanned all three figures. Their total distance moved was 615 km southwards, over 197 and 239 days respectively.

In the area east of Cape Hangklip, 6795 rock lobsters were tagged. Eighty-three were recaptured, and of these only three (3.6 %) moved from their site of release (Table 2.2).

The data provided by the Namibian Ministry of Fisheries and Marine Resources (MFMR) had complete information for only one fishing season (1986/87) and cannot be construed as representing the overall movement patterns that may have occurred. The movements that were recorded are presented in Fig.2.1. A total of 161 rock lobsters were tagged during this season, with 38 (23.6 %) tags being returned, of which 7 (18.4 %) had shifted more than 10 km from the area of release. Four of these rock lobsters were recorded as moving northwards, the furthest distance being 106 km, whilst three moved up to 14 km southwards. The average time-at-large was 156 days.

Table 2.1: Details of all recaptured rock lobsters for all fishing seasons on the West Coast. Average distance, and average distances moved per day are only calculated for those rock lobsters that were found to have moved between release and recapture. Average time-at-large are calculated for all recaptured rock lobsters

Fishing Season	Numbers not moving	Numbers moved North/West	Numbers moved South/East	Average Distance (km) ± S.E.	Average time-at-large (days) ± S.E. of rock lobsters that moved	Average time-at-large (days) ± S.E. of rock lobsters that did not move	Average distance (km) per day
68/69	1174 (100%)	0	0	0	-	130 ± 2.04	0
69/70	2841(100%)	0	0	0	-	144 ± 2.7	0
70/71	1773 (100%)	0	0	0	-	216 ± 4.1	0
71/72	1609 (100%)	0	0	0	-	203 ± 5.0	0
72/73	138 (100%)	0	0	0	-	609 ± 19.9	0
73/74	124 (90%)	8 (6%)	6 (4%)	18 ± 0	63 ± 12.6	643 ± 38.4	0.29
74/75	51 (85%)	7 (12%)	2 (3%)	18 ± 0	157 ± 6.4	595 ± 22.1	0.11
75/76	464 (100%)	0	0	0	-	193 ± 3.7	0
76/77	598 (90.7%)	5 (0.8%)	56 (8.5%)	19.6 ± 0.7	77 ± 9.2	85 ± 2.9	0.25
77/78	120 (100%)	0	0	0	-	113 ± 7.1	0
78/79	637 (100%)	0	0	0	-	139 ± 4.6	0
79/80	468 (100%)	0	0	0	-	186 ± 3.2	0
80/81	1773 (100%)	0	0	0	-	134 ± 2.6	0
81/82	1220 (99.92%)	1 (0.08%)	0	54 ± 0	50 ± 0	146 ± 1.9	1.08
82/83	896 (96.4%)	0	33 (3.6%)	43 ± 0	557 ± 15.4	263 ± 2.9	0.08
83/84	502 (100%)	0	0	0	-	428 ± 3.2	0
84/85	984 (100%)	0	0	0	-	93 ± 2.6	0
85/86	2993 (100%)	0	0	0	-	75 ± 4.5	0
86/87	2546 (100%)	0	0	0	-	173 ± 4.2	0
87/88	3328 (99.4%)	10 (0.3%)	11 (0.3%)	25.7 ± 1.3	311 ± 59.5	224 ± 3.5	0.08
88/89	2117 (99.52%)	3 (0.15%)	* 7 (0.33%)	23.12 ± 2.7	461 ± 131	257 ± 5.8	0.05
89/90	1252 (99.92%)	0	1 (0.08%)	94.8 ± 0	1020 ± 0	282 ± 8.6	0.09
90/91	1186 (99.58%)	5 (0.42%)	0	62.7 ± 19.6	625 ± 209.5	177 ± 6.0	0.1
91/92	1904 (97.19%)	34 (1.74%)	21 (1.07%)	31.8 ± 1.6	183 ± 28.4	149 ± 4.9	0.17
92/93	1957 (100%)	0	0	0	-	220 ± 4.0	0
93/94	1265 (100%)	0	0	0	-	313 ± 7.3	0
94/95	3138 (100%)	0	0	0	-	349 ± 5.0	0
95/96	1731 (100%)	0	0	0	-	330 ± 6.9	0
96/97	1453 (100%)	0	0	0	-	399 ± 8.2	0
97/98	1546 (100%)	0	0	0	-	418 ± 7.8	0
98/99	987 (100%)	0	0	0	-	382 ± 9.5	0
99/00	900 (100%)	0	0	0	-	375 ± 16.5	0
	43 675	**73**	**137**	**Average 48.9**	**Average 350.4**	**Average 263.8**	**Average 0.225**

* Excluding two rock lobsters moving > 500 km.

Table 2.2: Details of rock-lobster movements occurring east of Cape Hangklip.

Release Date	Release Area	Recovery Date	Recovery Area	Distance moved	Direction moved
09-10-1998	Kleinmond	15-03-2000	Hermanus	23 km	East
21-10-1999	Hermanus	11-01-2001	Gansbaai	17.5 km	East
21-01-2000	Kleinmond	11-01-2001	Gansbaai	32.5 km	East

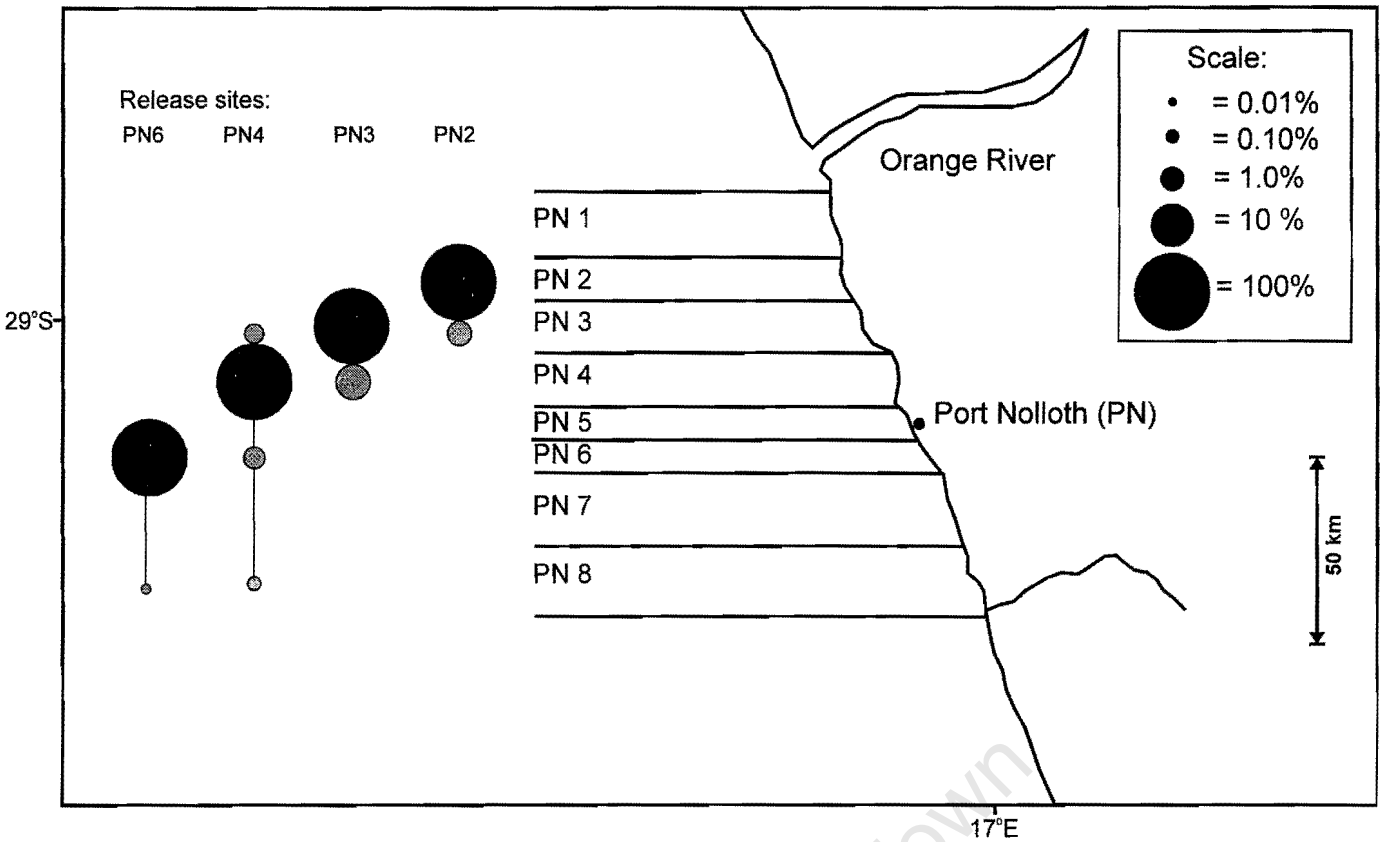

Fig. 2.1: Movements of rock lobsters occurring in the Port Nolloth area from1968/69 to 1999/2000.
Rock lobsters were released at each of the sites indicated and then recovered at the release site (black circles) or at other sites (grey circles). The diameters of the circles indicate the relative percentages recovered, according to the scale.

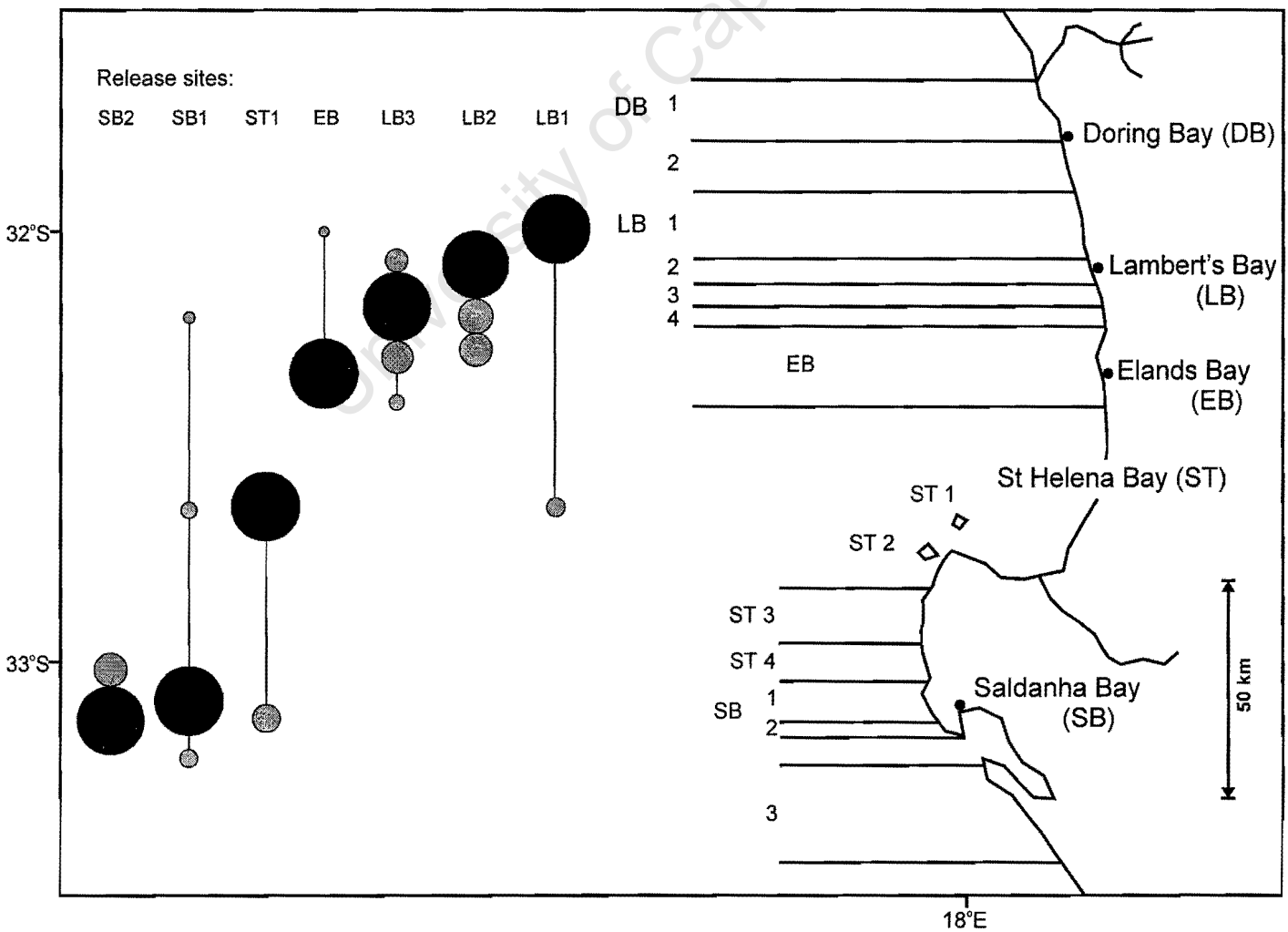

Fig. 2.2: Movements of rock lobsters occurring in the Doring Bay to Saldanha Bay area from 1968/69 to 1999/2000.
Rock lobsters were released at each of the sites indicated and then recovered at the release site (black circles) or at other sites (grey circles). The diameters of the circles indicate the relative percentages recovered, according to the scale.

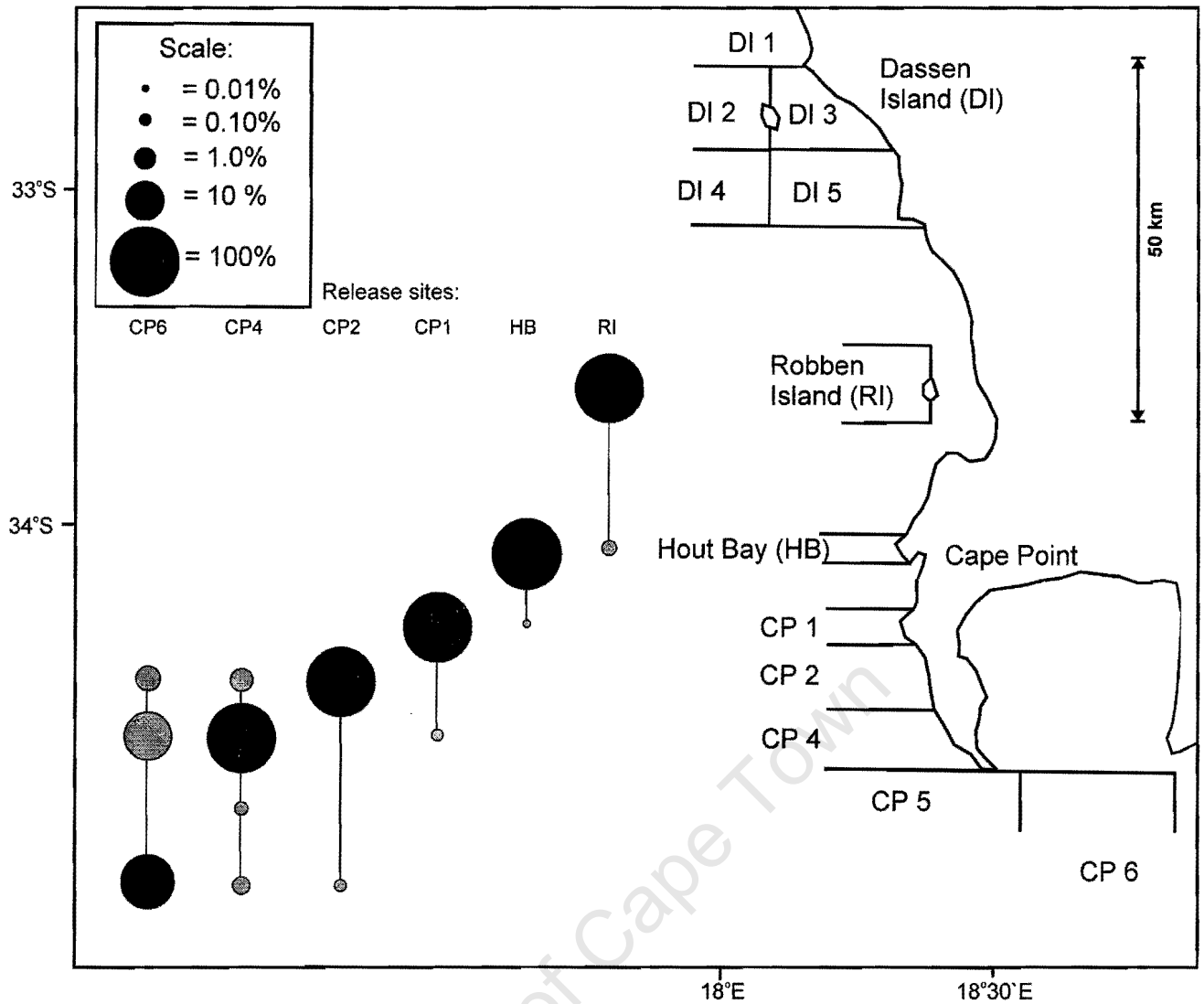

Fig. 2.3: Movements of rock lobsters occurring in the Cape Peninsular area from 1968/69 to 1999/2000.
Rock lobsters were released at each of the sites indicated and then recovered at the release site (black circles) or at other sites (grey circles). The diameters of the circles indicate the relative percentages recovered, according to the scale.

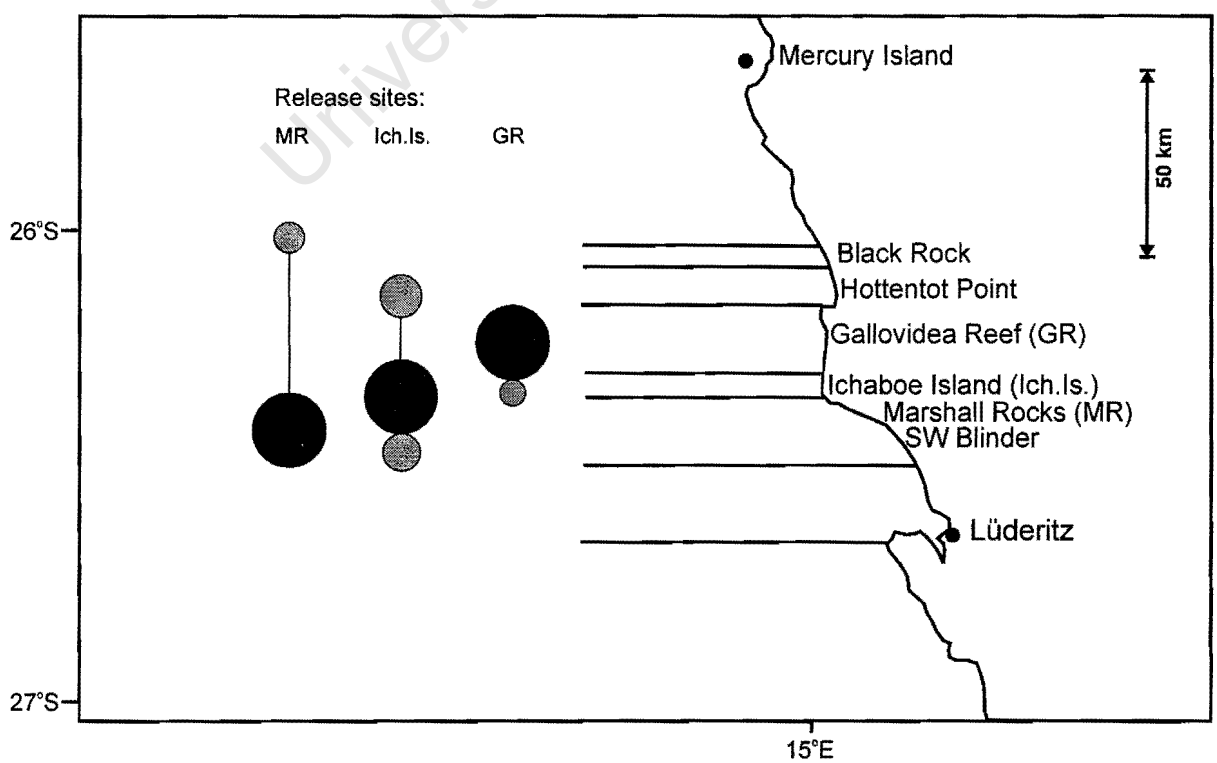

Fig. 2.4: Movements of rock lobsters occurring in the southern Namibian region in 1986/87.
Rock lobsters were released at each of the sites indicated and then recovered at the release site (black circles) or at other sites (grey circles). The diameters of the circles indicate the relative percentages recovered, according to the scale.

2.4 Discussion

The tag-recapture information from the West Coast of South Africa for 1968 – 2000, yielded a 0.5 % incidence of movement with 0.3 % of rock lobsters moving south-eastwards and 0.2 % north-westwards. Rock lobsters that did move from their release sites were calculated to move at a rate of 0.225 km/day over an average of 350 days-at-large. No rock lobsters moved distances greater than 10 km during 22 out of a possible 32 fishing seasons. Those rock lobsters not detected to have moved more than 10 km spent an average time of 264 days at large. During the ten fishing seasons that movements were detected, 137 rock lobsters moved south-east whilst just more than half that (73) moved north-west. Only two individuals were recorded moving southwards, covering a straight-line distance of 615 km each. It is probable that these two extreme distances were, in reality, due to error in recording the position of either release or recapture, rather than reflecting actual migrations.

Rock-lobster movements in southern Namibia during the 1986/87 fishing season showed that 18.4 % of tagged rock lobsters shifted more than 10 km. The greatest distance moved during this season was 106 km from Marshall Reef in the south to Black Rock in the north. The same fishing season in South Africa yielded no movements greater than 10 km for any tagged rock lobsters. Although substantially fewer rock lobsters were tagged in this season in Namibia than any season in South Africa, a high percentage of tags were recovered and a high percentage of rock lobsters had moved. Whether the contrast between South Africa and Namibia reflects genuine differences in movement rates is an open question. I believe it is more likely a reflection of the limited sampling in Namibia, and predict that more intensive tag-recapture studies in Namibia will yield results similar to those of South Africa.

Migration, as defined by Herrnkind (1980), is a direct locomotory movement of a distinct component of the population, within some confined time period, over relatively long distances. The movement detected on the West Coast of South Africa fails on this definition in that a "distinct component of the population" is required to have moved. From this data set I conclude that *Jasus lalandii,* or at least individuals larger than 75 mm CL, which are considered to be sexually mature, are not migratory and that there was no evidence of any distinct longshore migration between 1968 and 2000.

Groeneveld (in press) revealed a well-defined migratory pattern for *Palinurus delagoae* in a north-east direction along the east coast of South Africa. This migratory pattern was however confined to

juveniles, more specifically those < 55 mm CL, and the distances migrated spanned 20 - 495 km alongshore. This juvenile migratory pattern was only revealed due to the nature of the tagging operation conducted on this species. In the experimental trap-fishery for this species, lobsters of all sizes and both sexes are tagged, thus allowing monitoring of juvenile and adult males and females.

As only large, sexually mature, and mostly male *Jasus lalandii* are tagged (Goosen & Cockcroft 1995), the information gained from the tag-release program is limited to a particular group of the population. It is possible that smaller, sexually immature rock lobsters display migrations not detected by this study due to the nature of the data collected. It would be useful in future to tag a portion of all rock lobsters captured in traps, possibly using different colour tags for juveniles and females captured in different areas. However, because the fishery for *J. lalandii* is not simply an experimental one, but rather a large-scale commercial fishery, careful and thorough explanation of the importance of tag returns would have to be invested in the fishing community in order for such a tagging operation to be successful.

The Benguela current flows in a north-westerly direction along the West Coast of southern Africa. The distribution of a species can be displaced in the direction of the current transporting the larvae (Booth 1997). The West Coast of South Africa is considered to be the major breeding grounds of *J. lalandii*, hence larvae distributed by currents would be transported in a north-westerly direction. A contranatant (against the current) migration of adults to counter this is plausible and has been observed in several other species of lobster (*Palinurus gilchristi* - Groeneveld & Branch in press, *Jasus edwardsii* and *Jasus verreauxi* - Booth 1997). There was however no evidence of such movement detected for adult male *Jasus lalandii* in this study.

The dynamics of current flows are more complex than a simple flow in one direction. Eddies, recirculation, retroflection and counter currents usually occur (Booth & Ovenden 2000). Retroflection of the Agulhas current (flowing along the eastern coast of South Africa) occurs at the southern tip of the continent, carrying warm water back into the Indian Ocean. The retroflection is however unstable and large rings of warm water split away from the main current causing anomalous current reversals (Lutjeharms & Van Ballegooyen 1988). The anomalous weather patterns associated with the *El Niño* event in the Pacific Ocean in the early 1990's, may have induced changes in flow patterns of both the Benguela and Agulhas currents. In Western Australia, intrusions onto the shelf by the Leeuwin current have been associated with a very high level of larval settlement by coastal *P. cygnus* (Phillips & Pearce 1997). Similarly, deflections of both or either the Benguela or Agulhas currents could have resulted in high *J. lalandii* larval settlement on

the South-Western Cape coast of South Africa leading to the increased densities now being recorded east of Cape Hangklip. Once adults establish themselves in an area, larvae may be encouraged to settle close by (due to conspecific attraction) and, hence, a localized increase in population may occur. This hypothesis, however, requires further investigation and careful analysis of rock-lobster recruits and ocean current patterns.

Algal blooms (often referred to as "red tides") are a frequent occurrence on the West Coast of southern Africa due to the dynamics of the Benguela system there. During the early 1990's, the frequency of these algal blooms notably increased (Pitcher 1998), having a major disruptive effect on the marine life along this coast (Mathews & Pitcher 1996). Toxic algal blooms can cause mass mortalities of fish, shellfish, marine mammals, seabirds and even human deaths and illnesses. Non-toxic algal blooms also cause damage by clogging fish gills or, upon decay, causing anoxic water conditions (Pitcher 1998). Black mussels (*Mytilus meridionalis*), the favoured prey item of the rock lobster, also succumb to algal blooms due to a build up of toxins (Pitcher & Calder 2000). The effects of algal blooms are now known to extend beyond the obvious poisoning of fish and shellfish, and include more subtle effects on trophic structures. All sections of marine food webs are effected by harmful algal blooms, which can cause trophic dysfunction (Pitcher 1998).

An algal bloom occurring in the United States mid-Atlantic coast in 1985 caused large-scale mortalities, growth inhibition of bivalves and recruitment failure (Pitcher 1998). The increasing occurrence of algal blooms along the West Coast of southern Africa could be causing increasingly unsuitable benthic habitat for rock lobsters in this area. Rock-lobster larvae, if they have predictive settlement abilities, may choose not to settle in this area, but rather to recruit to other, more suitable areas. This would impact the amount of larval recruitment and hence, adult stock. The intense fishing pressure on the West Coast, coupled with a reduced larval recruitment could lead to a localized decline in adult rock-lobster stocks. There is however, as yet, no indication of reduced larval settlement in the area and further investigation is required.

Studies conducted during 1996 – 1997 show a distinct increase in the standing stock of *J. lalandii* in the area east of Cape Hangklip (Mayfield & Branch 2000), as was first proposed by Tarr *et al.* (1996). During studies to investigate the distribution range of *J. lalandii*, Heydorn (1969) noted that, "*J. lalandii* were observed in fair quantities in the Hangklip and Hermanus areas", yet in 1980 when Field *et al.* (1980) surveyed Betty's Bay, rock lobsters were virtually absent in this area. Currently their numbers have reached extremely high levels (Mayfield & Branch 2000). The question is: could the localized fluctuations in rock-lobster abundance be associated with natural

cycles? The answer is less easily provided. It is possible that localized, dense rock-lobster populations will naturally decrease as the rock lobsters eliminate food resources in the area and move to other areas. Concern has been expressed that the extremely high densities of rock lobsters now present east of Cape Hangklip may be causing irreversible damage to other species. In particular, radical declines of the urchin *Parechinus angulosus* and the winkle *Turbo cidaris* have occurred (Day & Branch 2000b). Reductions in grazers have been associated with a dramatic profusion of foliar algae and declines in encrusting coralline algae. As the latter are a settlement site for the abalone *Haliotis midae*, and juveniles of *H. midae* find vital concealment beneath urchins, these changes have immense implications for the abalone industry (Mayfield & Branch 2000; Day & Branch 2000a). Intense foraging of *J. lalandii*, need to be factored into management of both resources. Simply reducing the localized rock-lobster density may not be what is required. Fisheries management applications in the area should be holistically investigated, applied with added caution and closely monitored.

This chapter has examined all available large-scale tag-recapture data for *J. lalandii* on the West Coast of southern Africa and concludes that, at least in the case of adults > 75 mm in length, there is no evidence of any significant migration along the shore. This information eliminates the possibility of a south-eastward migration of adults from the West Coast to areas east of Cape Hangklip. Thus, it does not provide any explanation for the increase in density of rock lobsters in the South-Western Cape, but it does lead to further investigation of the movement patterns of *J. lalandii*:

1) A mesocosm study to examine levels of hole fidelity, diurnal activity, foraging behaviour and selection of shelter under intense threat of predation (Chapter 3).
2) Foraging behaviour in aquaria in the absence of predators (Chapter 5).
3) Detailed, seasonal monitoring of medium-scale movements of the rock-lobster population in the field, east of Cape Hangklip (Chapter 4), and a pilot study of acoustically tracking *J. lalandii* (Chapter 6).

Chapter 3

Movement patterns of *Jasus lalandii* in a mesocosmal experiment.

3.1 Introduction

Predation is a major force affecting the behaviour of many species (Spanier *et al.* 1998). There is increasing evidence that some species may be able to assess the risk of predation and change their behaviour accordingly, perhaps even permanently modifying it during their lifetime (Lima & Dill 1990). The presence of predators can thus influence prey to alter their natural behaviour and reduce the risk of predation. There are several ways in which spiny lobsters (sometimes called rock lobsters) reduce the risk of predation. Seeking shelter during the hours when predators are most active is a common way of achieving this (Spanier & Zimmer-Faust 1988; Spanier *et al.* 1998). An increase in lobster body size and gregarious behaviour also increases the chance of survival (Eggleston & Lipcius 1992). There is, however, a trade off between reducing the risk of predation and foraging successfully. Sheltering behaviour, or foraging near to shelter, reduces total energetic consumption and can reduce lobster growth rates (Lozano-Alvarez & Spanier 1997; Spanier *et al.* 1998).

Most studies of the movement patterns of spiny rock lobsters have revealed crepuscular foraging behaviour, with movement away from shelter occurring around sunrise and sunset (Spanier & Zimmer-Faust 1988; Jernakoff *et al.* 1987; MacDiarmid *et al.* 1991; Eggleston & Lipcius 1992; Spanier 1994). This is another means of reducing predation, because it exposes the lobsters at a time when visual detection will be difficult (Spanier & Zimmer-Faust 1988). In the absence of predators (under laboratory conditions), rock lobsters often leave the shelter of their dens to forage during the day (Lozano-Alvarez & Spanier 1997). During the mating season, individuals of *Jasus edwardsii* have often been observed out of their dens during daylight hours (MacDiarmid *et al.* 1991). Heydorn (1969) reported that *Jasus lalandii* undoubtedly feeds during both light and dark hours. It is known that activity patterns and foraging behaviour can be altered in the presence of predators (Spanier *et al.* 1998). However, if predators are scarce, rock lobsters may assess the predation risk to be low, and spend more time foraging, even during daylight hours. This type of behavioural modification is suggested by Lima and Dill (1990).

Jasus lalandii has been described as exhibiting homing movements (Heydorn 1969), with "homing" being defined as "periodic excursions from a home den or shelter to a foraging area and subsequent return to the original den or to a nearby den" (Jernakoff *et al.* 1987). Heydorn

(1969) further concluded that adult *Jasus lalandii* do not move extensive distances and exhibit no systematic natural migration. Seasonal patterns of movement onshore and offshore have been described for *J. lalandii* (Newman & Pollock 1971; see Chapter 2) but these movements were considered to be event-driven (by the appearance of oxygen-deficient water) and not a predictable migration. Rock lobsters are at their most vulnerable just after moulting when the shell is soft and movements are minimal. It would be expected that during this phase, rock lobsters would forage little and remain in their shelters. *J. lalandii* might thus show a high degree of fidelity to dens, especially during moulting and mating seasons, or when the risk of predation is high.

Numerous studies on a wide range of topics have been conducted on many species of spiny lobsters within aquaria and laboratories. These include studies on *Panulirus argus* (Lipcius & Herrnkind 1985); *Panulirus interruptus* (Zimmer-Faust & Spanier 1987; Spanier & Zimmer-Faust 1988); *Panulirus japonicus* (Koike *et al.* 1997), *Homarus americanus* (Barshaw & Able 1990; Moriyasu *et al.* 1995; Spanier *et al.* 1998), *Jasus verreauxi* (Montgomery & Brett 1996) and *Nephrops novegicus* (Newland & Chapman 1993).

Extensive investigations by Spanier and Zimmer-Faust (1988) on den selection by *Panulirus interruptus*, show that this lobster preferentially selects dens that provide shaded shelter and have two openings, thus allowing an escape route. Shading, and hence low light intensity inside *vs.* outside the den, strongly influenced den selection.

For some species of rock lobsters, conspecific odour is an attractant and causes aggregation, (Zimmer-Faust & Spanier 1987) although the presence of predators and the size of the shelter can influence the extent of aggregation (Eggleston & Lipcius 1992). Eggleston and Lipcius (1992) found that when conspecific density was high and predation risk low, lobsters showed the highest potential for gregariousness and aggregated in large shelters but when conspecific density and predation risk were simultaneously both high, lobsters shifted to gregarious habitation of smaller shelters. Gregariousness has been shown to enhance survivorship because predators are more readily detected and prevented from entering to shelters (Eggleston & Licius 1992). Although *J. lalandii* is not considered gregarious and has never been known to form aggregations to deter predators, individuals are seldom found far from other conspecifics. This type of aggregation may be as a result of animals sharing a resource even if they are not gregarious by nature (Zimmer-Faust & Spanier 1987).

Movement, growth and mortality studies of many organisms are usually conducted by means of a tagging system (Moriyasu *et al.* 1995) allowing researchers to recognize individual animals. However, in any tagging study, it is important to investigate firstly, how the tag will affect the individual and secondly, the probability of the tag being lost (Montgomery & Brett 1996). Tag loss may be caused by tag-induced mortality, death from natural causes, tag shedding or dispersal of tagged individuals out of the study area (Montgomery & Brett 1996). The temporary tagging method used in this study has not previously been used on *J. lalandii* although similar tagging methods have been employed in two studies on *J. edwardsii* (MacDiarmid *et al.* 1991; Kelly 1999). My study thus included an assessment of the suitability of antennal tags for studies in the field. The tags were evaluated for ease of reading, retention and the practicalities of using this tagging technique in the field.

This chapter details a study conducted in the Kelp Forest tank of the Two Oceans Aquarium, Cape Town, South Africa. In many respects the Kelp Forest tank simulated the natural habitat of the West Coast rock lobster, *Jasus lalandii,* and therefore provided an opportunity to examine the behaviour of rock lobsters under controlled but quasi-natural conditions. The tank did, however, contain large numbers of predatory fish and the lobsters experienced predator-dominated circumstances. Aspects of hole fidelity, diurnal activity, foraging behaviour and shelter selection were examined under these conditions of high predation threat. It was hypothesized that 1) the rock lobsters would display high levels of fidelity to shelters, 2) that they would be more active in foraging at dusk and dawn, 3) that aggregations of rock lobsters would occur in large rather than small shelters and 4) that the presence of food would influence the rate at which the rock lobsters left their shelters.

From the onset of this experiment, it was clear that the results obtained would be preliminary. Although conducting studies in the Kelp Forest tank had many advantages, there were also several unavoidable disadvantages. The positive aspects of using the Kelp Forest tank included a quasi-natural, but fully controlled environment with continuous access (no weather constraints for diving), and the fact that the size of the rock-lobster population was defined and every individual in the population could be tagged and monitored. The disadvantages of conducting experiments in such an environment included not being able to manipulate conditions to test variable factors. More important was the inability to have replicate tanks or a control tank in which the density of predators could be held at levels approximating natural conditions. It is for these reasons that the results presented are conservatively interpreted.

3.2 Methods

The study took place in the Kelp Forest tank at the Two Oceans Aquarium, Cape Town, South Africa during May, June and July 1999. The Kelp Forest tank is a public display within the aquarium aimed at illustrating the natural marine life found within typical West Coast kelp beds. The dimensions of the tank are approximately 10 m X 10 m X 6 m deep. The display has been in existence since 1995 and many species of reef fish are represented (e.g., Red Roman – *Chrysoblephus laticeps*, Red Stumpnose – *Chrysoblephus gibbiceps*, Poenskop – *Cymatoceps nasutus,* White Steenbras – *Lithognathus lithognathus*, Hottentot – *Pachymetopon blochii*). Kelp (*Ecklonia maxima* and *Macrocystis angustifolia*), red and green algae and numerous invertebrate species complete the display. The estimated density of large predatory fish in the Kelp Forest tank was 14 fish per 600 cubic meters of water. The bottom of the tank comprises approximately 50 % sand and 50 % rock debris. Seawater is continuously pumped from the adjacent harbour, filtered and adjusted to approximately 12°C. A wave-generator creates gentle water movement within the tank. Direction of water flow was tested using coloured dye ejected from syringes, but there appeared to be no predictable direction of water flow within the tank. Large fiberglass moulds mimic rock structures and closely resemble natural shallow reefs in Western Cape waters. To prevent the rock lobsters from "disappearing" into the hollow fibre-glass 'rocks', the entrances to the interior of these structures were closed by securing plastic mesh across them.

A benthic survey of the tank showed an abundance of drift kelp (*Ecklonia maxima*) accumulating inside larger holes. Green filamentous algae (*Cladophora* spp.) were abundant on the fiberglass structures and found growing around the perimeter of the entrance to most shelters. The inside of shelters were barren except for the presence of a single sponge colony. Ribbed mussels (apart from those provided as part of the experiment) occurred in the holdfasts of *E. maxima*. Due to the ongoing replacement of these kelp plants by aquarium staff, ribbed mussels were unintentionally, periodically introduced.

Using baited commercial rock-lobster fishing traps, 110 rock lobsters (55 males and 55 females, 70 - 95 mm CL), were captured over two days from the West Coast of South Africa. These lobsters were immediately transported to the aquarium where they were tagged with coloured cable-ties (zip-ties 104 mm long by 2.5 mm wide) secured around the base of the antennae. Seven different colour cable-ties, threaded with coloured plastic tubing, provided a large number of unique colour combinations. One cable-tie with coloured plastic tubing was attached to one antennae and another cable-tie, that lacked plastic tubing, was attached to the second antennae of each rock lobster. The excess cable-tie was trimmed off after it was secured around the base of

the antennae (Fig. 3.1). Each rock lobster had a unique colour combination, which allowed subsequent non-disruptive identification of individual rock lobsters (see MacDiarmid *et al.* 1991 for method). Tagged rock lobsters were placed in plastic crates within the kelp tank to allow recovery, acclimitisation and protection from the predatory reef fish. After a 24-hour recovery period, the rock lobsters were released from the crates and thereafter left undisturbed. Food was provided in the form of ribbed mussels (*Aulacomya ater*), which were positioned under a mesh roof where they were accessible to the rock lobsters throughout the experiment, but could not be eaten by the fish.

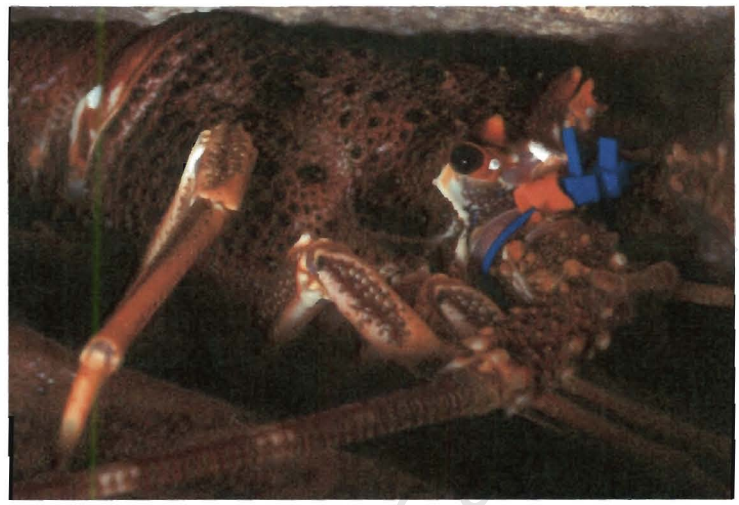

Fig. 3.1: *Jasus lalandii* with antennal cable-tie tags used for this study. Specific individual's colour code = Blue-Red-Blue.

After seven days, all shelters in the fibre-glass rocks that were selected for occupation by rock lobsters were numbered with plastic-coated lead markers and classified into caverns (≈ 2 m^2), large (≈ 1 m^2) or small (≈ 0.5 m^2). To monitor fidelity to shelters and frequency of foraging, every numbered hole was searched every two to three days to record the location of each lobster, and any newly occupied holes were numbered. The remaining area of the tank was also searched for rock lobsters not sheltering in holes. In addition to these searches, to detect diurnal movements, four 48-hour observation sessions were conducted, during which divers recorded the rock lobsters present in each numbered hole every four hours and searched the tank for moving rock lobsters. This allowed comparisons between day and night movement behaviour. The ribbed mussels were moved to a different location on the bottom of the tank on day 22 of the experiment, the aim of which was to determine if the position of olfactory food stimuli influenced rock-lobster movement. The entire experiment lasted 44 days, during which 64 individual periods of observation were conducted.

As the experiment progressed, it became evident that few rock lobsters were foraging at all, regardless of where the ribbed mussels were placed. In an attempt to confirm that the rock

lobsters were not responding to olfactory stimuli, a perforated jar with pilchard chunks (a strong olfactory stimulus) was used as bait to test if this would lure rock lobsters out of their shelters. Between two of the underwater observation sessions, the jar with pilchard chunks was placed in an area that could be visually monitored from outside the tank and was within 1.5 m of a shelter known to contain at least five rock lobsters at the time. The jar and surroundings were continuously observed from outside the tank (to prevent any disturbance) for two hours to detect if there was any movement out of shelters associated with foraging.

3.2.1 Tethering

Ten rock lobsters (72 – 83 mm CL) were tethered on either sand or rock debris substrate, to confirm the predatory effects of the high densities of predators. Each rock lobster was individually tethered to a 30-cm long monofilament line secured around the carapace and attached to a 1 kg lead diving weight by means of a swivel, which would allow the rock lobster movement in any direction but prevented them from gaining access to shelter. A total of 4 rock lobsters were tethered over sand and 6 over rock debris. The tethering took place between 14:30 and 15:30 and predation was monitored for 18 hours.

3.2.2 Dietary Analysis

Once all other experiments within the tank were complete, 24 of the remaining rock lobsters were recaptured to examine stomach contents. The rock lobsters were anaethetised through immersion in an ice-water slush and their stomachs removed. The stomachs were blotted dry and weighed to an accuracy of 0.001g using an electronic balance (Mettler AE 100). The stomach contents were flushed into a Petri dish, the stomach membrane re-weighed and the gut-fullness index calculated after Hyslop (1980) and Williams (1981):

$$\frac{\text{total stomach weight (g)} - \text{stomach membrane weight (g)}}{\text{total stomach weight (g)}} \times 100$$

Stomach contents were viewed under a Nikon binocular dissecting microscope (8 X magnification) and diagnostic fragments identified. An independent Student's t-test was used to compare the means of gut-fullness indices between aquarium and wild rock lobsters, which were captured in the same area at the same time of year, and were of the same size class (70 – 85 mm CL) as those in the aquarium (Mayfield *et al.* 2000a & b).

3.2.3 Statistical Analysis

All data were tested for normality and homogeneity by Kolmogorov-Smirnov procedure and Levene's test (Zar 1984) and alpha was set at 0.05. Where necessary, data were either log or (log + 1) transformed for normality or homogeneity. A dependant Student's t-test was used to determine if there was a significant difference in the frequency of occurrence of rock lobsters in each shelter type during the day and night. A fixed effects modal, two-way ANOVA was used to test the frequency of distribution of rock lobsters between shelter types and between day and night. A G_{adj} statistic for the log-likelihood ratio, a goodness of fit test (Zar 1984) was used to test if the numbers of animals leaving or moving to caverns, large or small shelters, departed significantly from a random pattern. In the case of departures from each of these types of shelters, the expected ratios were calculated from the proportions of lobsters originally occupying each shelter type. For lobsters moving into either caverns, large or small shelters, the expected proportions arriving were assumed to be equal on the assumption that the total areas covered by each shelter type in the tank were equal. Williams' correction factor (Fowler & Cohen 1995) was used in all one-way classifications yielding the G_{adj} statistic. An independent Student's t-test was used to determine if there was a significant difference in the gut-fullness index for aquarium held *vs.* free-living rock lobsters. All statistical tests were applied through StatSoft, Inc 1995 STATISTICA for windows.

3.3 Results

Of the 110 tagged rock lobsters introduced to the tank, 53 could not be tracked for the full duration of the experiment (six weeks). Twelve of these 53 rock lobsters were known to have lost at least one tag and, although they were often re-sighted, their movements could not be accurately tracked. The remaining 41 of these rock lobsters were either never re-sighted following release or were re-sighted on less than 3 occasions (5 %) and were excluded from any further analyses. The 57 rock lobsters that were monitored regularly during the 64 observation counts (both day and night) were seldom seen moving about the tank outside the shelters (Table 3.1). No more than 3.41 % of the lobsters were ever observed moving around the tank during any particular observation period, and the frequency of movement declined with time.

Table 3.1: Numbers of rock lobsters observed moving out of shelters, during 48-hour periods of the experiment. Percentage of all rock lobsters sighted moving in the 48 hours are indicated in brackets.

Time period (days)	Number of rock lobsters moving
5 - 7	16 (3.41 %)
12 - 14	5 (1.05 %)
26 - 28	2 (0.43 %)
40 - 44	1 (0.35 %)

Although rock lobsters were seldom seen outside of shelters, the frequencies of those that were detected to have moved from one shelter to another was determined (Fig. 3.2). No rock lobster exchanged shelters more than twice in the duration of the experiment and most rock lobsters did not move at all (Fig. 3.2).

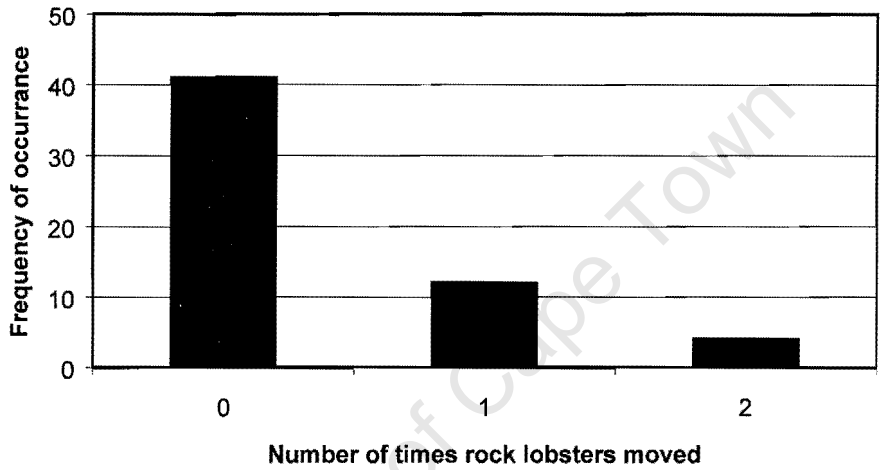

Fig. 3.2: Frequency of rock lobsters moving once, twice or not at all (n=57).

Sixteen rock lobsters were observed to have exchanged shelters during the experiment (Fig. 3.2). After dividing the experiment duration (44 days) into 4-day time blocks, the frequency with which the lobsters moved various distances was calculated. The overall instances of movement are indicated in Fig. 3.3. Rock lobsters spent most of their time not moving. When they did move, they did so rapidly and again remained in the newly occupied shelter for a lengthy period of time.

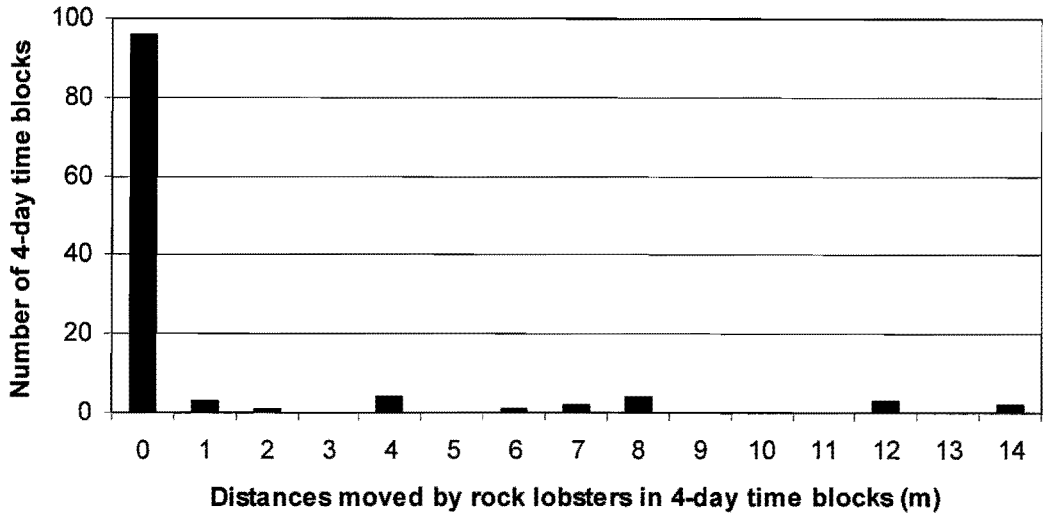

Fig. 3.3: Instances of the number of time blocks in which rock lobsters moved and the distances these rock lobsters moved (n=16).

A dependent Student's t-test between equal numbers of day-night observations made during the four 48-hour observations showed no significant difference between frequency of occurrence in holes during the day *vs.* the night ($t_{0.05,30} = 0.94$, $p = 0.35$, data were log+1 transformed, Fig. 3.4). Most rock lobsters congregated in cavern-like hollows (floor area approximately 2 m^2) despite the fact that the total areas covered by caverns, large and small holes were approximately equal (Table 3.2). A fixed effects modal, two-way ANOVA showed a significant difference in frequency of distribution between the shelter type, but no significant difference between day and night and, no significant interaction between shelter and day/night (Table 3.3). A post-hoc Tukey test showed a significant difference between cavern shelters *vs.* large shelters and small shelters, but no significant difference between large and small shelters (Table 3.3). Frequency of occurrence in large and small holes was similar in value (Fig. 3.4).

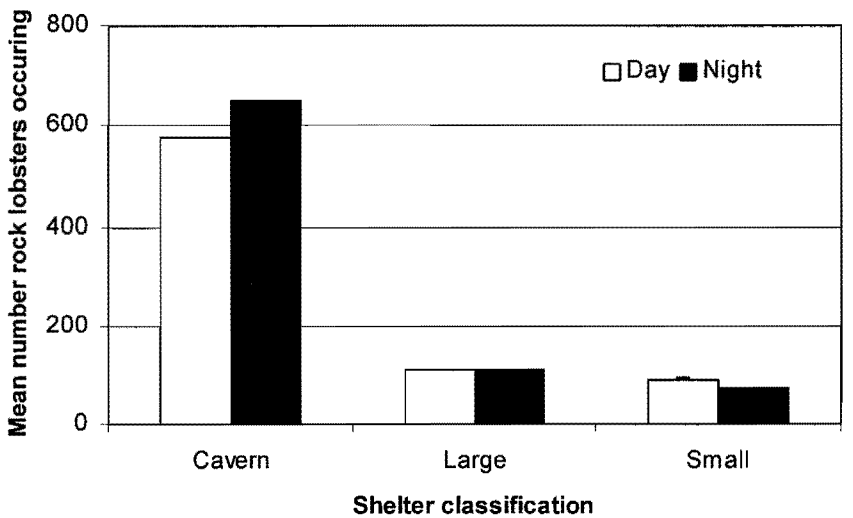

Fig. 3.4: Occurrence of rock lobsters in different hole types. Cavern ≈ $2m^2$, Large ≈ $1m^2$, Small ≈ $0.5m^2$. (n=53, 48 observations).

Table 3.2: Distribution of shelter types in the Kelp Forest tank and area covered by each shelter type.

Hole Type	Cavern	Large	Small
Number occurring in tank	5	8	18
Approximate area per hole	$2m^2$	$1m^2$	$0.5m^2$
Total area covered in tank	$10m^2$	$8m^2$	$9m^2$

Table 3.3: Results of two-way ANOVA with fixed effects between shelter type (n=3) and day/night (n=31) and post-hoc Tukey test to show significant differences between shelter conditions.

Two-way ANOVA							
	df effect	MS effect	df error	MS error	F	p-level	
Shelter	2	29.823	56	1.025	29.08	$\ll 0.01$	Significant
Day/Night	1	3.273	56	1.025	3.19	0.08	Not significant
Shelter x Day/Night	2	0.333	56	1.025	0.32	0.72	No interaction
Post-Hoc Tukey test							
Cavern *vs.* Large			$p \ll 0.001$				Significant
Cavern *vs.* Small			$p \ll 0.001$				Significant
Large *vs.* Small			$p = 0.07$				Not Significant

A log-likelihood ratio, goodness of fit test (G – statistic) was used to test the null hypothesis that there was no difference in the ratios of rock lobsters leaving (moving from) cavernous, large or small shelters. A second log-likelihood ratio was used to test the null hypothesis that there was no difference in the ratios of rock lobsters entering (moving to) cavernous, large or small shelters (Table 3.4). William's correction factor (Fowler & Cohen 1995) was applied for the one-way classification yielding G_{ajd} (the adjusted value of G), which was used as the test statistic. Significantly more lobsters moved from large and small shelters than was expected, whilst significantly more moved into caverns, than into either small or large shelters (Table 3.4).

Table 3.4: Results of log-likelihood ratio of rock lobsters moving from or to shelters. H_0: no difference in ratios of rock lobsters leaving or entering cavernous, large or small shelters.

Moving FROM:

$p < 0.05$, d.f. = 2	Cavern	Large	Small	
Observed	13	3	5	21
Expected	17.6	1.88	1.5	21
2 x G	-3.94	1.4	6.02	6.96
Williams' correction factor				1.032
G_{ajd}				**6.74**

Moving TO:

$p < 0.05$, d.f. = 2	Cavern	Large	Small	
Observed	15	3	3	21
Expected	7	7	7	21
2 x G	11.43	-2.54	-2.54	6.35
Williams' correction factor				1.032
G_{ajd}				**6.15**

Although no specific direction of water current was detected within the tank, olfactory stimuli provided by the presence of ribbed mussels did not induce the rock lobsters to leave their shelters, nor to move towards the food source. Throughout the duration of the experiment, no lobsters were seen foraging on the mussels or moving towards them. The relocation of the mussels did not induce any change in behaviour of the rock lobsters. Even when a perforated jar with pilchard chunks was placed 1.5 m from a shelter, the rock lobsters did not move out of the hole.

3.3.1 Tethering

All four rock lobsters tethered over the sand substratum were eaten within three hours of being tethered (Fig. 3.5). During this period, reef fish (Red Roman, Red Stumpnose, Poenskop) were frequently seen attacking the lobsters. Once the lobsters had been demobilized, other fish participated in feeding on the rock lobster. Half of the rock lobsters tethered over the rocky substratum survived for up to 18 hours. There was no evident relationship between size or sex of the rock lobsters that survived tethering. Rock-lobster mortality was higher on sandy substrate than on rocky substrate.

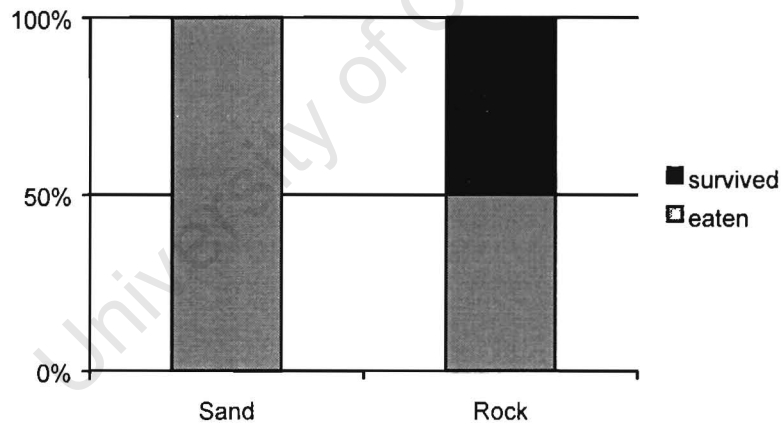

Fig. 3.5: Proportion of rock lobsters eaten when tethered over rocky or sandy substrata (n = 10).

3.3.2 Dietary analysis

The primary food source of the rock lobsters within the Kelp Forest tank was algae. Sponge and ribbed mussel contributed a small amount to the diet, as indicated by the benthic survey and Fig. 3.6. Three individual rock-lobster stomachs contained mesh, similar to that used by fishermen. The mesh was assumed to have been ingested before the lobsters were introduced to the aquarium and retained in the guts because it could not be digested. Of the prey items present in the stomachs, only four (ribbed mussel, winkle, coralline algae and polychaete tube) were not

available to the lobsters in or near their shelters (Fig. 3.6). These items constituted less than 15 % by frequency to the diet.

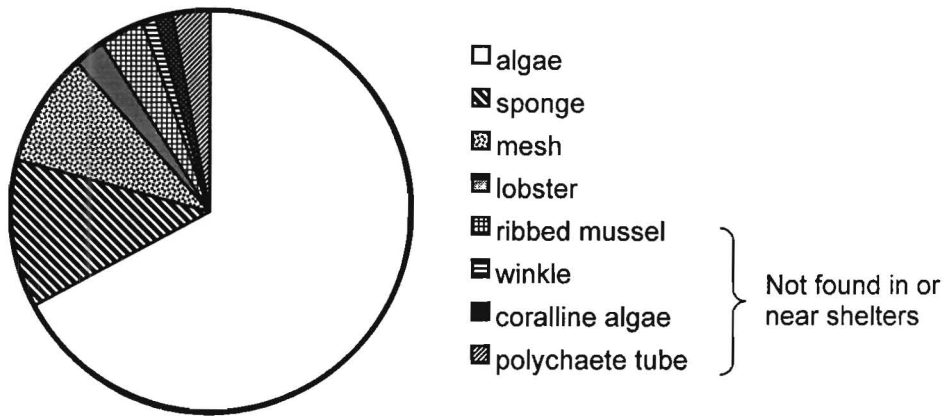

Fig. 3.6 Diet, by frequency of occurrence, of rock lobsters within the Kelp Forest tank (n = 24).

The average gut-fullness index for aquarium held rock lobsters was 13.9 g (± S.E. 0.173) and for wild rock lobsters, 40.8 g (± S.E. 0.192). Wild rock lobsters had significantly higher gut-fullness indices when compared to rock lobsters from the tank (independent Student's t-test: $t_{0.05,40} = -4.1$, $p \ll 0.001$, data were log transformed).

3.4 Discussion

The antennal tags used in this study are temporary, and I would expect them to be shed at the first moult. They are external and have no internal attachment. Due to this, their effects on the rock lobster are limited. A study on the effects of capture and tagging using a similar method of tagging concluded that "tagging had no effect additional to initial capture which itself had only short-term effects" (MacDiarmid *et al.* 1991). There were no apparent mortalities directly due to tagging. Only the low light levels inside the shelters hampered the accurate recording of the tagged rock lobsters. During daylight observations, the coloured tags were easily visible with no disturbance to the lobsters. However, during night observations, the colours were difficult to read. By using strongly contrasting colours this problem could be overcome. Colours that were strongly contrasting were easy to accurately read. Seventy-seven percent of the tags were retained for the length of time required to track movements. The tagging method was thus considered suitable for utilisation in further field studies.

Many studies have shown that the foraging behaviour of spiny lobsters can be altered by the presence of predators (Spanier *et al.* 1998; Lozano-Alvarez & Spanier 1997; Eggleston & Lipcius 1992). The foragers may trade off the conflict between obtaining food against the risk of

predation (Spanier *et al.* 1998). In the Kelp Forest tank at the Two Oceans Aquarium, predatory fish constituted a demonstrable threat to rock lobsters. Lobsters that were tethered and could not escape into shelters, suffered high mortalities. The threat of predation in the Kelp Forest tank was unquestionably high, illustrated by the tethering results (Fig. 3.5). As the experiment progressed, fewer rock lobsters were observed moving out of shelters (Table 3.1). The reasons for the observed decrease in movements through time, could be either due to a decreasing number of rock lobsters remaining in the tank, or those that did move, got preyed upon and thus eliminated, inducing less activity of the lobsters in the tank. High numbers of predatory fish were present and under these conditions the rock lobsters displayed high fidelity to shelters with only 16 lobsters (28 %) exchanging shelters. Only four rock lobsters exchanged shelters twice, which was the highest number of moves recorded for this study (Fig. 3.2). The intense levels of predations in the tank almost certainly created artificially high levels of fidelity to shelters.

Jasus lalandii displayed no evidence of crepuscular foraging in this study (Fig. 3.4) as has been described for several other spiny lobster species (*Panulirus* spp. – Jernakoff 1987, *Jasus edwardsii* – MacDiarmid *et al.* 1991). There was no significant difference between the number of lobsters occurring in shelters during day or night (Table 3.3; Fig. 3.4). Lobsters are known to leave their dens and forage during the day (Heydorn 1969; MacDiarmid *et al.* 1991; Lozano-Alvarez & Spanier 1997), but usually when there is little or no predation pressure. Lima and Dill (1990) suggest that animals can assess predation risk and adapt their behaviour accordingly. There was undoubtedly an intense risk of predation in the Kelp Forest tank, which appears to have induced a short-term change in behaviour pattern in rock lobsters. If they left the protection of the den to forage, the risk of being preyed upon would have been very high. Even after a considerable length of time spent under high predation risk (44 days), foraging beyond the confines of shelters was extremely limited.

Rock lobsters can survive long periods of rough weather at sea without feeding (Heydorn 1969). It is also well documented that *Jasus lalandii* ceases foraging prior to and just after moulting (Heydorn 1969; Beyers *et al.*1994; Mayfield *et al.* 2000a). It is therefore not unusual that rock lobsters have extended periods when they do not feed. Thus, under unfavourable conditions, rock lobsters are not compelled to forage. The dietary analysis clearly indicated that rock lobsters in the aquarium predominantly fed on algae (Fig. 3.6). Algae were abundant and could be utilised without leaving the protection of dens. More than 85 % of the diet comprised items available in shelters (Fig. 3.6) and rock lobsters were rarely observed beyond the confines of shelters (Fig. 3.2; Table 3.1). Thus, the frequency of foraging outside shelters was considered to

be very low. Kelp is known to form a natural portion of the diet of rock lobsters (Heydorn 1969). However, it has never been considered to be a favoured food item and Mayfield *et al.* (2000a) classify it as a minor part of the diet. The diet of rock lobsters in the tank was made up of nearly 65% algae (Fig. 3.6), indicating that when under high predation risk, rock lobsters can utilise alternate food sources. Barkai and Branch (1988) first reported evidence of rock lobsters utilising unorthodox food sources, including kelp. However, the enzymes required to break down the Laminaria and alginate in the algae, are not present in the digestive fluid of the rock lobster (Barkai *et al.* 1996). This suggests that rock lobsters are primarily carnivores, not being able to fully digest plant material. *Jasus lalandii* are considered to be "opportunistic scavengers which may shift to other, less palatable or less energetically rewarding, food items when necessary" (Barkai *et al.* 1996).

Four of the prey items present in the lobsters' gut contents could not have been obtained in or near any holes (Fig. 3.6), indicating that the rock lobsters must have moved from their shelter to forage on these items. The chance of these prey items being remnants from field foraging (before capture) is negligible as rock-lobster digestion rate is much faster than the 44 days that rock lobsters were in captivity (Zoutendyk 1988). A small percentage (28 %) of the rock lobsters did exchange shelters during the study and could have foraged on items outside of shelters during these movements (Fig. 3.2).

Milton (1953) analysed the organic content of *Ecklonia* spp. and although the protein content was only 7.1 %, there were several trace elements that were present in high concentrations (iron, zinc, strontium, manganese and iodine). Kelp is rich in carbohydrates and fiber. Although kelp, and other seaweeds, do not appear to be essential components of the rock-lobsters diet, simple, non-polymeric sugars may be released as algae is ingested (Barkai *et al.* 1996). In this study, rock lobsters largely consumed food available within shelters, algae made up the bulk of the diet, and the lobsters survived on this diet for the 44-day duration of the experiment.

The significant difference in gut-fullness index between aquarium-held rock lobsters and those captured from the wild, indicates that the aquarium rock lobsters were not foraging to their maximum potential. The rock lobsters introduced to the aquarium were not nearing any moult cycle that would have naturally prevented them from feeding. It is thus assumed that under the high predation risk, the rock lobsters restricted their rate of feeding and made opportunistic use of prey items available in or near to shelters.

Saila and Flowers (1968) reported that ovigerous rock lobsters move very little, but that once their eggs are released, they resume normal foraging and shelter-seeking movements. It is possible that in my mesocosmal study, the limited foraging of female rock lobsters could have been attributed to their ovigerous state. However only a small number of monitored rock lobsters in this study were ovigerous (16 %) and the non-ovigerous females and the male lobsters also displayed limited movement similar to those of ovigerous females. It is thus unlikely that the ovigerous females biased the observed movement patterns.

Aggregations of rock lobsters formed in large cavernous shelters in the Kelp Forest tank. Aggregations are often formed when lobsters are under threat of predation (Eggleston & Lipcius 1992) and gregariousness enhances survival (Zimmer-Faust & Spanier 1987). Although no aggressive displays towards the predators were observed in my experiment, the clumping of individuals supports the "selfish herding" theory (sensu Hamilton 1971) where an individual reduces its own risk of being eaten by positioning itself among conspecifics. When divers approached aggregations of rock lobsters in shelters, the rock lobsters displayed the defensive behaviour of "raised cephalothorax, antennae pointing towards the source of irritation and twitching" (Heydorn 1969). Significantly more rock lobsters moved out of large and small shelters than out of caverns (Table 3.4) whilst significantly more rock lobsters moved into caverns than into either large or small shelters (Table 3.4). Thus, rock lobsters chose caverns over both large and small shelters, even though the total areas available in caverns, large and small shelters were similar (Table 3.2). This indicates that the rock lobsters selected to aggregate in caverns, at least under the conditions of high predation threat that existed in this experiment.

Twenty-eight percent of rock lobsters in this study exchanged shelters (Fig. 3.2), but it is evident that the rock lobsters remained within the protection of shelters most of their time (Fig. 3.3). When a movement was detected to have occurred, it was over a short period of time. Once the lobsters had secured shelter after moving, they remained in this newly occupied shelter for a lengthy period of time before moving again, if at all (Fig. 3.3). This behaviour pattern further emphasises the limitation that high predation threat appears to have imposed on the movement and foraging of rock lobsters within the Kelp Forest tank.

The central findings of this study are thus:

- The tagging method used was effective and considered feasible for application in the field.
- Under intense predation levels, rock lobsters displayed high levels of hole fidelity and there was no evidence of diurnal movement patterns.
- Rock lobsters largely consumed food available within shelters, thus the bulk of their diet was made up of algae.
- Rock lobsters aggregated selectively in large cavernous shelters.

Although the experiment in the Kelp Forest tank yields some interesting findings, there are limitations on the broader application of the results. Replication of the experiment was not possible, as only one such Kelp Forest tank exists. The densities of predators in the tank were unnaturally high compared to their current levels in the wild, although it should be noted that substantial depletions (75 – 99 %) of predatory fish have taken place over the past 100 years (Griffiths 2000). Although it would have been ideal to remove predators from the tank in order to repeat the experiment without this factor, this was not possible because the tank, first and foremost, serves the purpose of being a display tank in a public aquarium. Nevertheless, the experiments conducted in the Kelp Forest tank generated conclusions that are valid within these limitations, and two further studies flowed from it:

- The level of fidelity to holes was examined in a field study using the tagging method evaluated in this chapter (Chapter 4).
- A series of experiments were conducted on the behaviour of rock lobsters in an aquarium tank that lacked predators (Chapter 5).

Chapter 4

Field monitoring of seasonal rock-lobster (*Jasus lalandii*) movements and abundance, with comparisons between reserve and non-reserve areas.

4.1 Introduction

Rock lobsters are large, mobile and benthic and many species are known to migrate 10's to 100's of kilometers over weeks or months (MacDiarmid *et al.* 1991). Migrations may occur on a seasonal basis (*Panulirus argus, Jasus edwardsii*), in response to weather changes (*Homarus americanus*), or may be size-dependant (*Palinurus delagoae*). Interspersed with migrations are periods of relatively little movements. These are often dictated by natural cycles of moulting and reproduction, which can greatly influence daily activity patterns (Herrnkind 1980; Lipcius & Herrnkind 1985). Laboratory studies have shown behavioural changes linked to moulting and reproduction (Paterson 1969), but the influences of the extrinsic environment during these natural cycles are less well documented.

Newman and Pollock (1971) documented distinct inshore movements of *Jasus lalandii* on the West Coast of South Africa during the summer months. These inshore migrations were, however, strongly linked to low-oxygen events associated with the decay of algal blooms (Chapter 2). The rock lobsters moved into shallow water in an attempt to escape the anoxic waters further offshore. Identical seasonal migrations were detected in *Jasus lalandii* populations off the Namibian coast where similar seasonal anoxic conditions occur (Tomalin 1993; Grobler & Noli-Peard 1997). These event-driven inshore migrations of *J. lalandii* applied to males and females of all sizes and were not related to any intrinsic behavioural cycles. For these reasons, it cannot be assumed that all populations of *J. lalandii* will undergo seasonal inshore–offshore migrations. However, the rigorous annual moult cycles of adult lobsters suggest the potential for intrinsic patterns of movement, associated with moult cycles. Males of *J. lalandii* moult predominantly between November and January whereas females moult between May and July (Heydorn 1969). Cannibalism of recently moulted individuals has been observed under aquarium conditions (Heydorn 1969; Paterson 1969). The vulnerability of recently moulted rock lobsters suggests that males and females, having different moult cycles, should separate before moulting. Heydorn (1969) noted a "spreading out" of the population during peak moulting periods, suggesting that shortly before moulting, the rock lobsters seek protective shelter, isolation and calm waters. Rock lobsters would thus be expected to move inshore to sheltered areas shortly prior to moulting and males and females should have different cycles of

inshore movement, leading to fluxes in sex ratios at specific times. Monitoring natural populations in the field and in the absence of anomalous environmental effects is required to resolve whether or not *J. lalandii* seasonally migrate inshore-offshore in a manner linked with its moult cycle.

Data used to detect migratory movements are often collected by monitoring commercial catch rates of the species. There is, however, evidence that traps that are used to fish for lobsters, do not sample a representative portion of the population (Newman & Pollock 1974). Movements in response to baited traps may further bias the movements of individuals within a population, as Jernakoff and Phillips (1988) found when investigating the foraging range of *Panulirus cygnus.* Analysing movements based on tag and recapture data poses problems of interpretation (reviewed by Herrnkind 1980). Visual examination by divers yields data on abundance of lobsters, locations and sociality, without removing the lobsters from the environment and is also well suited to the study of local movement patterns over seasonal periods (Herrnkind 1980).

Palinurid homing movements are defined by Herrnkind (1980) as being "periodic, often daily, excursions from a shelter to some nearby area, with subsequent return to that shelter or others nearby". Clawed lobsters such as *Homarus americanus* (Karnofsky *et al.* 1989), and spiny lobsters such as *Panulirus argus* (Herrnkind 1980) and *Jasus edwardsii* (MacDiarmid *et al.* 1991; Kelly 1999) have been classified as displaying homing movement patterns. Early behavioural studies of *J. lalandii* report the species to be gregarious, but large males are often solitary and occupy holes that they actively defend (Heydorn 1969). This suggests that after foraging trips away from a hole, large males will return to the same hole, hence displaying homing tendencies. Aquarium studies (Chapter 3) showed that under threat of intense predation, *J. lalandii* displayed high levels of fidelity to shelters. Field investigations under more natural levels of predation are clearly needed to determine if rock lobsters behave in the same manner under natural conditions.

Among numerous other functions, marine reserves provide an environment in which populations that are not exposed to fishing pressures can be monitored and their behaviour compared to that in fished areas (Childress 1997). Several studies investigating the effects of marine reserves on the populations of spiny lobsters have shown that lobster size and abundance are generally greater within marine reserves compared to fished areas nearby (MacDiarmid & Breen 1992; Babcock *et al.* 1999; Edgar & Barrett 1999; Kelly *et al.* 2000). Marine reserves protect the ecosystem from degradation caused by fishing, and may enhance the quality and abundance of

prey items available to rock lobsters (Roberts in press). It could be concluded that rock lobsters residing within marine reserves would have a rich diet and, hence, a faster growth rate, as has been indicated by Babcock *et al.* (1999), Kelly *et al.* (2000) and Roberts (in press).

In this chapter, I describe a field study of rock-lobster abundance and small-scale movement patterns, conducted in an area where an increase in rock-lobster abundance has been observed in the last decade (Mayfield & Branch 2000). The study investigated levels of hole and site fidelity, seasonal abundance of male and female rock lobsters and seasonal fluctuations in size and sex of rock lobsters and compared these factors between a site in a marine reserve and a site that lay beyond the bounds of the marine reserve. It was hypothesized that:

1) Rock lobsters will display high levels of hole fidelity (based on the findings of Chapter 3). Failing this, there should be high levels of site fidelity.
2) Seasonal inshore–offshore movements would occur corresponding to natural moult and reproductive cycles and would yield fluxes in male to female ratios that would be similar in the reserve and the fished areas. Rock lobsters were expected to move inshore shortly before moulting. For females, this would occur between May and July, and for males, between November and January.
3) The reserve would have a higher rock-lobster density and average size than the non-reserve site.
4) Rock lobsters in the area will have lower gut-fullness indices than those from the West Coast where prey availability is higher (Barkai *et al.* 1996; Mayfield *et al.* 2000a & b) and the prey composition will differ, for similar reasons, to that of previous *J. lalandii* diet studies.

4.2 Methods

The study was conducted in the field at Betty's Bay in the South-Western Cape, east of Cape Hangklip. The primary study site lay on the eastern side of Stony Point in Betty's Bay, which is the western boundary of the H. F. Verwoerd Marine Reserve (Fig. 4.1). Except for limited shore angling, no other fishing is allowed within the reserve which thus offers protection to all species. A preliminary survey of the area showed that an abundance of male and female rock lobsters of all sizes occurred there. The site could be accessed by boat or from the shore, and was not excessively exposed to prevailing winds or swell. These prerequisites were essential for the feasibility of the study.

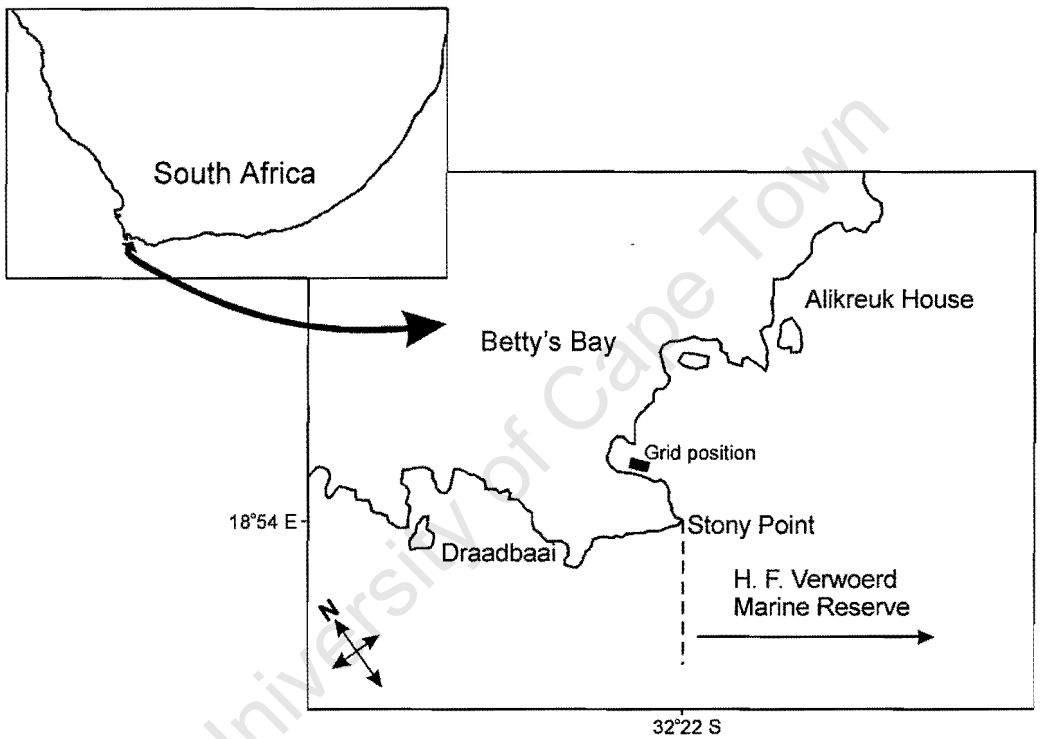

Fig. 4.1: Map showing positions of three study sites on the South-West Cape coast of South Africa. The black block represents the relative position of the underwater grid at the Stony Point study site.

To study small-scale movements and hole or site-fidelity, the Stony Point study site was demarcated using an underwater grid (Fig. 4.2). An area stretching 50 m along the shore and 25 m seawards was marked with cement mounds every five meters. Each cement mound was marked with a labeled perspex disk, secured to an eyebolt, which was anchored in the cement. A binding compound, Chryso Aquabeton, from Chryso Southern Africa (Pty) Ltd, was mixed into the cement to prevent underwater wash-out and promote rapid hardening of the cement. The cement markers formed an underwater grid, which allowed divers to easily identify their position in the survey site. To guide divers conducting underwater searches, metal chains were attached to eyebolts in the cement markers along three of the six 50 m lines, formed by the grid. Divers

could thus follow the chains when surveying the site. The underwater grid was used to seasonally monitor the size and activities of rock lobsters occurring in the area. To follow the movements of lobsters and their hole or site-fidelity, a representative sample of rock lobsters occurring in sub-areas of the grid were tagged with antennal tags (see Chapter 3) to allow individual recognition by divers. All statistical tests were applied through StatSoft, Inc. 1995 STATISTICA for windows.

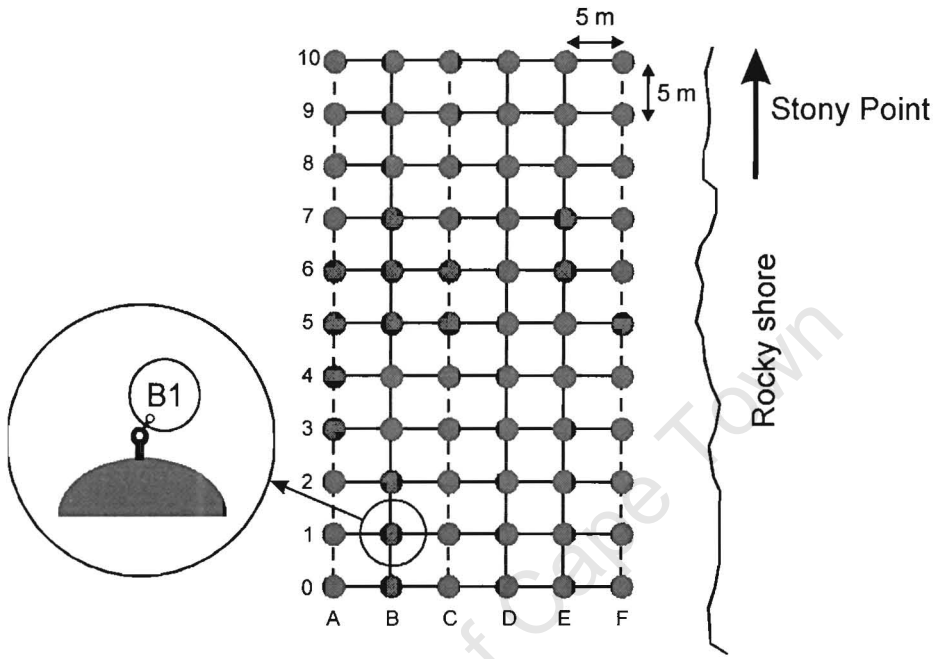

Fig. 4.2: Diagrammatic representation of underwater grid and cement mounds with labeled perspex disks located at Stony Point study site. Dashed lines represent chains linking eyebolts through lines A, C and F.

4.2.1 Monitoring sizes and activities

Each month (January to December 2000) all rock lobsters occurring within a 2-m radius of each of the 66 cement markers within the underwater grid (Fig. 4.2) were counted. This procedure covered an area of 829 m^2, i.e. 66 % of the possible 1250 m^2 covered by the entire grid. The lobsters were classified as being small (< 40 mm CL), medium (41 – 80 mm CL) or large (> 80 mm CL). Divers also recorded the activity of each lobster located, i.e., whether it was sheltering in a hole, moving about the reef, or feeding. Most lobsters observed feeding were out of holes. Any antennally-tagged rock lobsters encountered on these surveys were also recorded and were incorporated in the antennal-tag monitoring results. Each rock-lobster size class was tested separately for a seasonal change in abundance, using a one-way ANOVA. The seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). All data were tested for normality and homogeneity by Kolmogorov-Smirnov procedure and Levene's test, and alpha was set at 0.05.

4.2.2 Dietary analysis

A dietary study was undertaken of rock lobsters at two sites in the H. F. Verwoerd Marine Reserve, i.e. Stony Point and Alikreuk House, to establish the amounts and types of prey consumed by rock lobsters in the area. In February 2000, 20 male rock lobsters > 75 mm CL were captured from Alikreuk House and 15 from Stony Point. All rock lobsters were captured by hand just after dawn at a depth of 3 – 5 m. The stomachs were removed from the rock lobsters and frozen. For analysis, the stomachs were defrosted, blotted dry and weighed to 0.001 g using an electric balance (Mettler AE 100). The stomach contents were then flushed into a Petri dish and the stomach membrane re-weighed. Stomach contents were viewed under a Nikon binocular dissecting microscope (8 X magnification) and diagnostic fragments used to identify prey. Each stomach was subjectively assessed in order to estimate the percentage contribution of each prey species relative to the total gut volume. The gut-fullness index of each stomach was calculated (see Chapter 3 for details) following the methods of Hyslop (1980) and Williams (1981) and mean indices for the two areas compared using an independent Student's t-test. Data were log transformed for normality and homogeneity according to Kolmogorov-Smirnov procedure and Levene's test, and alpha was set at 0.05.

4.2.3 Effects of antennal tagging

Although a study conducted by MacDiarmid *et al.* (1991), in which a similar tagging method was used, suggested that the tags did not impede the animal in any way and would be moulted off at the next ecdysis, the effects of the tag on the rock lobsters were tested under laboratory conditions. To test if antennal tagging caused mortality and whether the tags were shed with ecdysis, 20 female pre-moult rock lobsters were antennally tagged using coloured cable-ties (zip-ties) secured around the base of an antennae (see Chapter 3, Fig. 3.1) and held in aquaria for eight weeks over the period they were likely to moult (May to July). An additional 20 females that were not tagged were held under identical conditions and were monitored as control animals. The rock lobsters were held in individual tanks and monitored until they had moulted. Moulting success, tag shedding and survival of rock lobsters were monitored daily.

4.2.4 Field tagging and monitoring

Two methods were used to capture rock lobsters for antennal tagging. Initially, perforated jars baited with pilchard were used to lure rock lobsters out of shelters. A diver then systematically hand-captured several rock lobsters at a time from the vicinity of the jars and delivered them to a boat anchored above. The lobsters were tagged using coloured cable-ties (zip-ties) secured

around their antennae (see Chapter 3, Fig. 3.1) to allow individual identification. To prevent light-induced eye damage (Meyer-Rochow 1994) the lobsters were shaded from the sun whilst being tagged. Once tagged, a diver returned the lobsters to an area similar to where they were captured. Re-sightings of the 216 rock lobsters tagged in this manner were recorded during monthly surveys conducted in the underwater grid, as described above. Because the area in which tagged rock lobsters were released was sub-sampled (only 66 % of the area was searched), only 66 % of tagged rock lobsters were expected to be re-sighted. In reality, far fewer than the predicted 66 % were re-sighted (see Results) probably because they had been disturbed too much by the procedures employed.

Because of this very low rate of re-sightings, another capture method, involving less disturbance, was employed in an attempt to increase the rate of re-sightings. This involved antennal tagging that was conducted entirely underwater (after Kelly 1999) with one diver hand-capturing each lobster and another diver securing the tag, measuring and sexing the lobster. Lobsters were only captured and tagged if they were found within a pre-determined, demarcated area within the underwater grid (two 10 X 10 m demarcated blocks, Fig. 4.3). Once details were recorded, each lobster was returned to the same hole from which it was captured. These lobsters were therefore, far less disturbed. The method was time consuming, so only 86 lobsters could be tagged, but re-sightings were more frequent. Two batches of underwater antennal tagging were conducted, one in February (Batch 1) and one in April (Batch 2). The results are presented separately.

The subsequent monitoring protocol was also changed. Only the two 10 X 10 m blocks identified and demarcated within the underwater grid (Fig. 4.3) were searched for tagged rock lobsters each month. Fourteen holes occupied by tagged rock lobsters were individually labeled with numbered cable-ties secured around the nearest kelp stipe. The grid locations or hole numbers of all antennally-tagged rock lobsters occurring within the two 100 m^2 blocks were recorded monthly.

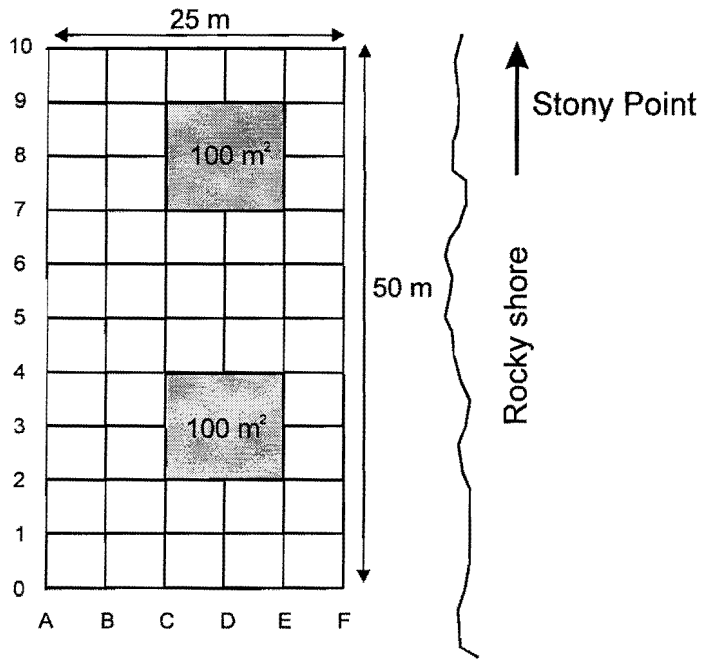

Fig. 4.3: Diagrammatic representation of two 10 m X 10 m blocks, demarcated for tagging and monitoring antennally-tagged rock lobsters, in relation to the underwater grid located at Stony Point study site.

4.2.5 Population monitoring

Two 200 m X 100 m sites within the Betty's Bay area were identified as suitable for conducting monthly population monitoring of rock lobsters. The first site, Draadbaai (Fig. 4.1), was outside the H. F. Verwoerd Marine Reserve, approximately 2 km westwards of the original Stony Point study site. The second site, Alikreuk House (Fig. 4.1), was within the H. F. Verwoerd Marine Reserve, approximately 4 km eastwards of the Stony Point study site. Each month (February 2000 – January 2001) two divers hand-captured all the lobsters they encountered within each of the areas, measured and sexed them, then released them where they had been caught. The catch-per-unit-effort (CPUE) was defined as the number of rock lobsters captured per diver per minute. Whilst the lobsters were out of the water, they were kept under a shade cloth so as to prevent damage to the retina (Meyer-Rochow 1994). Although only two sites were examined in this study, it was specifically designed to complement a much larger series of comparisons between reserve and non-reserve areas conducted by Mayfield *et al.* (in press). For statistical analysis, all data were tested for normality and homogeneity by Kolmogorov-Smirnov procedure and Levene's test and alpha was set at 0.05. Data from the closed and open recreational fishing seasons at both the reserve and non-reserve sites were further tested using the heterogeneity chi-square analysis for homogeneity (Zar 1984).

4.3 Results

4.3.1 Monitoring sizes and activities

There were no obvious trends in the abundance of small, medium or large rock lobsters during the 12-month sampling period over four seasons (Fig. 4.4). A separate one-way ANOVA for each size class over the four seasons showed no significant difference in the numbers of rock lobsters occurring in each season over the 12-month period (small: $F_{3,8} = 0.55$, $p = 0.7$; medium: $F_{3,8} = 3.33$, $p = 0.08$; large: $F_{3,8} = 1.85$, $p = 0.23$). The overall low abundance observed in May can be attributed to poor weather conditions during this month and, hence, difficulty in sampling. Throughout the sampling period large individuals were the least-encountered lobsters and medium-sized individuals were most abundant except in October and November, when small rock lobsters were slightly more abundant (Fig. 4.4).

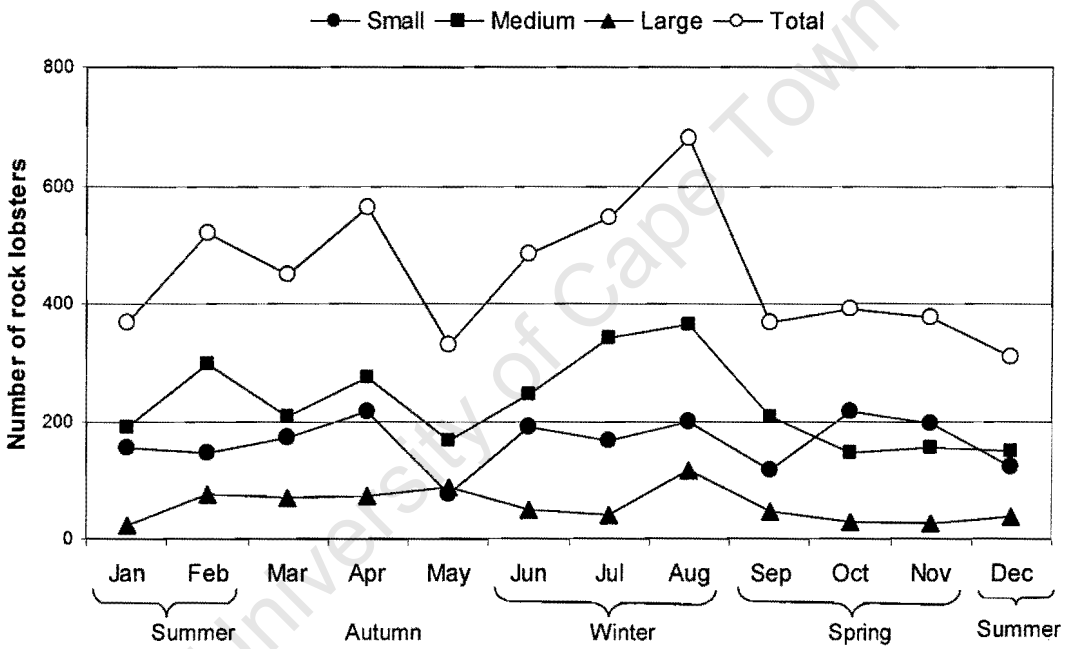

Fig. 4.4: Abundance profile and size compilation of rock lobsters at Stony Point during Summer, Autumn, Winter and Spring. Small = < 40 mm CL, Medium = 41 – 80 mm CL, Large = > 80 mm CL.

Throughout the 12-month sampling period, most rock lobsters were observed in holes (Fig. 4.5). Overall, the percentage of small lobsters observed out of holes was 0 – 30 %, with even fewer feeding (Fig. 4.5 A). Medium rock lobsters were also seldom observed outside shelter, and less than 20 % were seen feeding (Fig. 4.5 B). Large rock lobsters were more frequently recorded out of holes (15 – 35 %) than either medium or small lobsters. Large and medium-sized rock lobsters were more frequently seen feeding than small individuals (Fig. 4.5).

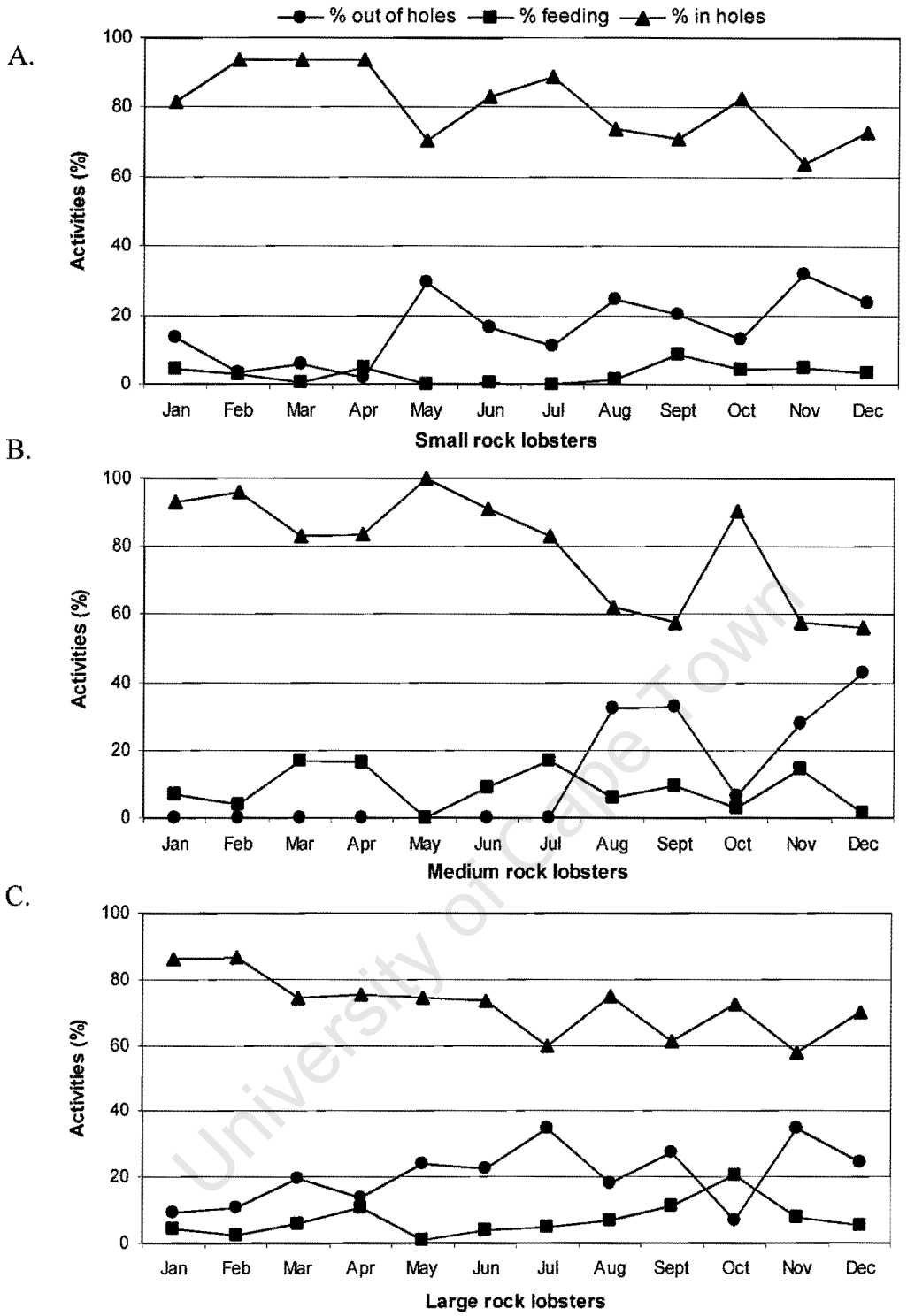

Fig. 4.5: Activity profiles of small, medium and large rock lobsters at Stony Point, January to December 2000.

4.3.2 Dietary study

The average gut-fullness index for lobsters foraging at Stony Point was 38.63 % ± 5.09 S.E. and for those foraging at Alikreuk House, 27.62 % ± 6.91 S.E. There was no significant difference in rock-lobster gut-fullness indices between Stony Point and Alikreuk House sites (independent Student's t-test: $t_{0.05, 29} = 1.66$, $p = 0.12$). Analyses of diagnostic fragments showed the rock-lobsters diet consisted largely of algae (most obviously at Stony Point), with sponges,

crustaceans and molluscs making up other large portions (Fig. 4.6). Moderate amounts of coralline algae were found in the diet of rock lobsters from the Stony Point site, whereas lobsters at Alikreuk House additionally consumed barnacles and fish (Fig. 4.6). Urchins comprised a very small proportion of the diet at both Stony Point and Alikreuk House.

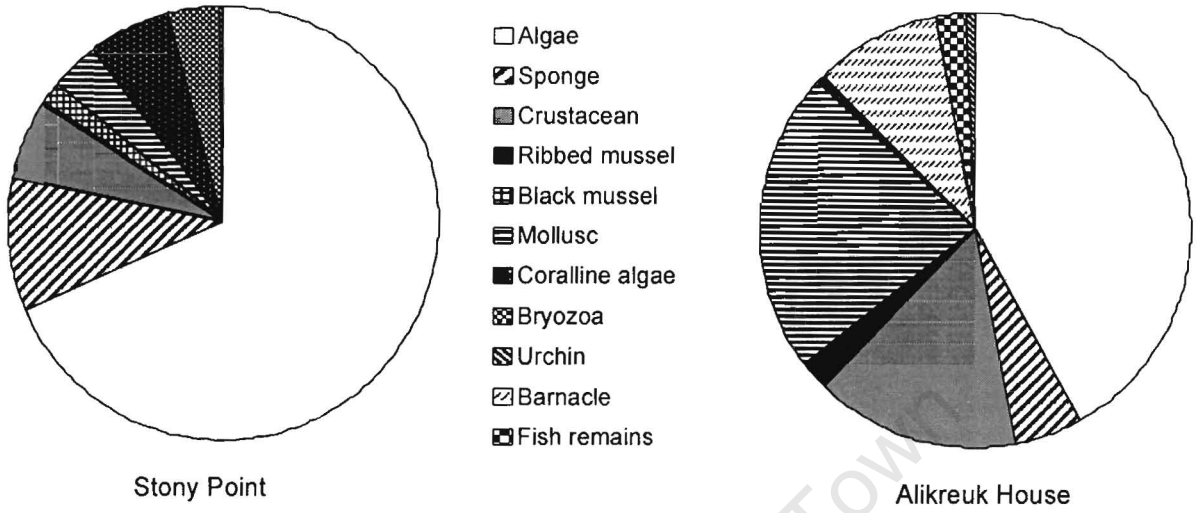

Fig. 4.6: Frequency of occurrence of different food items in the diet of rock lobsters at Stony Point (n = 15) and at Alikreuk House (n = 16).

4.3.3 Effects of antennal tagging

All antennally-tagged rock lobsters survived the eight week experiment yielding a 100 % survival rate of tagged individuals. The survival rate of the control (untagged) rock lobsters was, however, only 90 %. All tagged rock lobsters that moulted during the experiment, successfully moulted off the temporary tag with no mortalities occurring.

4.3.4 Field tagging and monitoring

Of the 216 rock lobsters initially tagged using the baited-capture method, only a total of 31 (14 %) were re-sighted during the six months of observation, with a mere four individuals being sighted more than once. Because only 66 % of the area was being searched, it was expected that a maximum of 66 % of the tagged lobsters would be re-sighted each month. This baited-capture method, however, yielded, at most, 7 % re-sightings of male rock lobsters in any particular month (Fig. 4.7). Too few female rock lobsters were re-sighted to be analysed. The percentage of re-sightings continued to decrease over time with the last individual being sighted in June. The percentages of re-sightings were clearly far lower than expected.

Re-sightings of rock lobsters tagged using the underwater tagging method had higher returns (Fig. 4.8; Fig. 4.9) and I consider these results more valid because the tagging method was less disruptive to the rock lobsters. The first batch of rock lobsters tagged underwater comprised 27 males and 11 females tagged in February 2000. Of these, 25 (66 %) were re-sighted at some stage. The percentage re-sightings initially increased from March to May when 40 % of males and 20 % of females were re-sighted. After that, re-sightings decreased until the last female was re-sighted in June and the last male in August (Fig. 4.8). Five rock lobsters from Batch 1 were observed over 4 to 6 months, last being sighted in August, after which no tagged rock lobsters were seen. The remaining lobsters were re-sighted between one and three times.

The second batch of rock lobsters tagged underwater comprised 24 males and 24 females, which were tagged in April 2000. Of these 48 rock lobsters, 20 (42 %) were re-sighted. Thirty-three percent of the males were re-sighted in May and 21 % of the females in May and June (Fig. 4.9). A steep decrease in re-sightings of males occurred between May and June after which re-sightings of both male and female rock lobsters decreased, with the last tagged rock lobster being sighted in August.

Mature female rock lobsters undergo ecdysis annually between May and July whereas males moult between November and January (Heydorn 1969). Laboratory studies showed that antennal tags were successfully moulted off at the next moult. As the monitoring of tagged individuals spanned January to September, it was expected that re-sightings of tagged females would decrease after their moult period. However, although re-sightings of females did decrease during this time, re-sightings of males, which were not undergoing ecdysis at any stage during the monitoring, decreased similarly. Thus, moulting, and hence tag shedding, is unlikely to be an explanation for the decline in sightings (Fig. 4.8; Fig. 4.9).

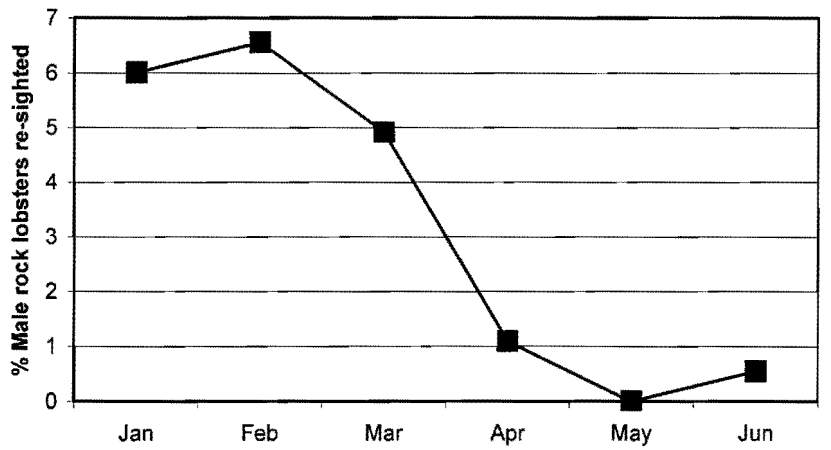

Fig. 4.7: Percentage re-sightings of male rock lobsters from initial baited-capture and tag method. Males tagged = 183, Females tagged = 33

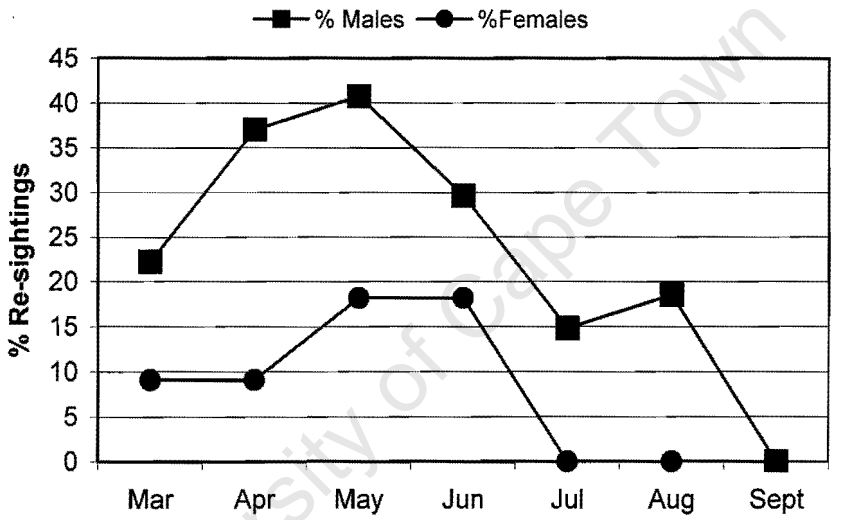

Fig. 4.8: Percentage re-sightings of male and female rock lobsters from Batch 1 of the underwater tagging method. Males tagged = 27, Females tagged = 11.

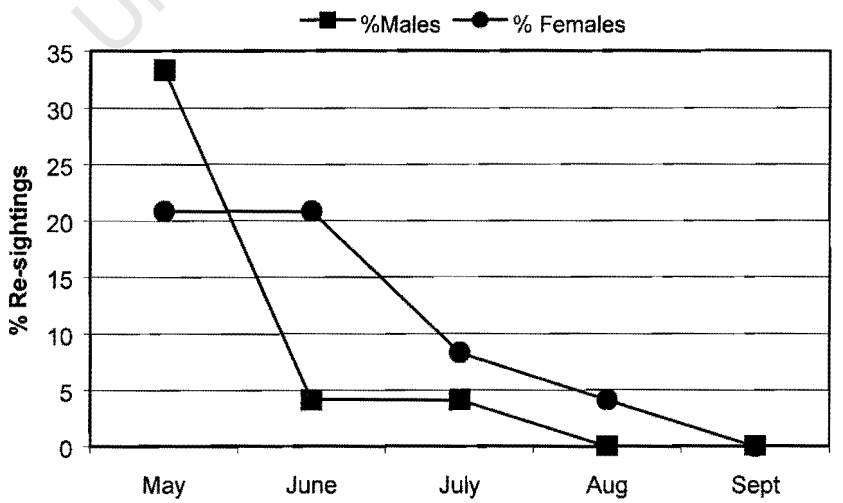

Fig. 4.9: Percentage re-sightings of male and female rock lobsters from Batch 2 of the underwater tagging method. Males tagged = 24, Females tagged = 24.

The direct linear distances moved by tagged rock lobsters between sightings were plotted in categories (< 1m, 1m – 5m, 6m – 10m, and 11m – 15m) according to their frequency of occurrence (Fig. 4.10). Most rock lobsters moved between 1 – 5 m between re-sightings. One rock lobster, tagged in Batch 1, moved up to 15m between two sightings (Fig. 4.10).

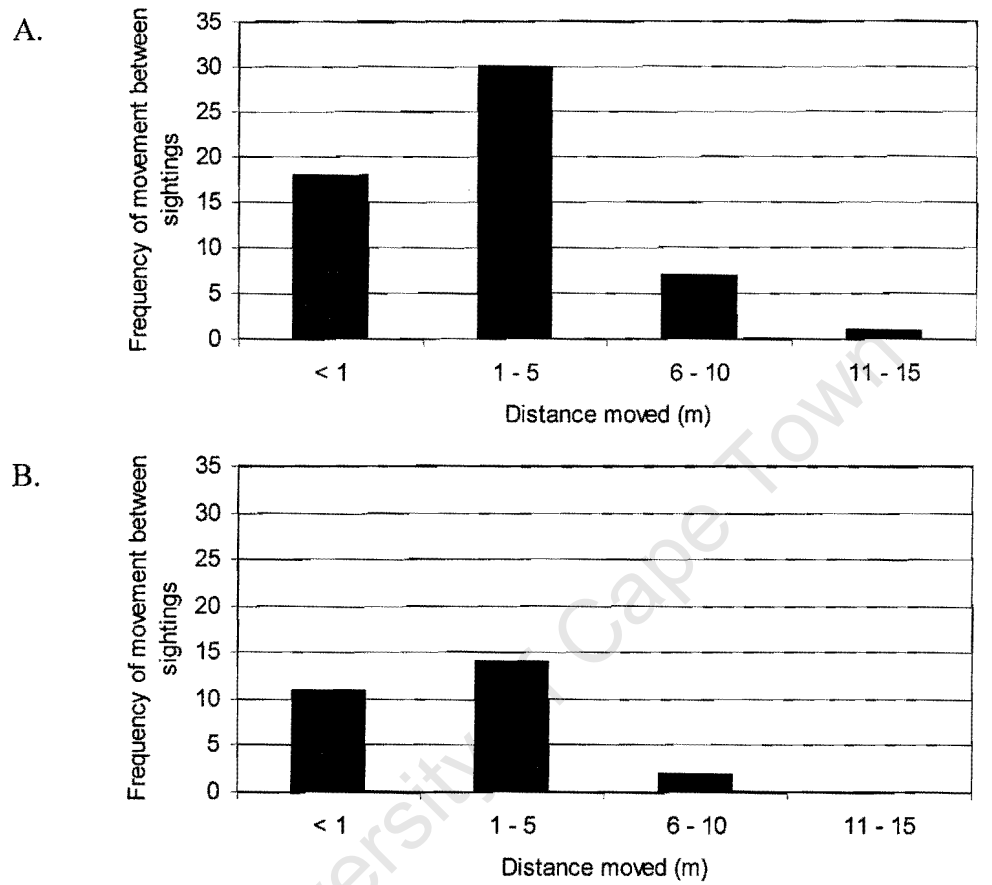

Fig. 4.10: Frequency of distances moved by rock lobsters between monthly sightings. A) Rock lobsters re-sighted tagged in Batch 1 (n = 38), B) Rock lobsters re-sighted tagged in Batch 2 (n = 48).

Over the entire period, only two tagged rock lobsters were ever re-sighted in the same hole on consecutive occasions. All remaining tagged lobsters showed no fidelity to any particular hole. Of the 14 holes monitored monthly, solitary lobsters most frequently occupied the shelters and many shelters were often vacant (Fig. 4.11). However, on 45 % of occasions, between two and seven lobsters were seen communally sheltering in a hole (Fig. 4.11). When shelters were shared, the rock lobsters were usually of similar size and were never seen displaying aggressive behaviour towards each other (pers. obs.).

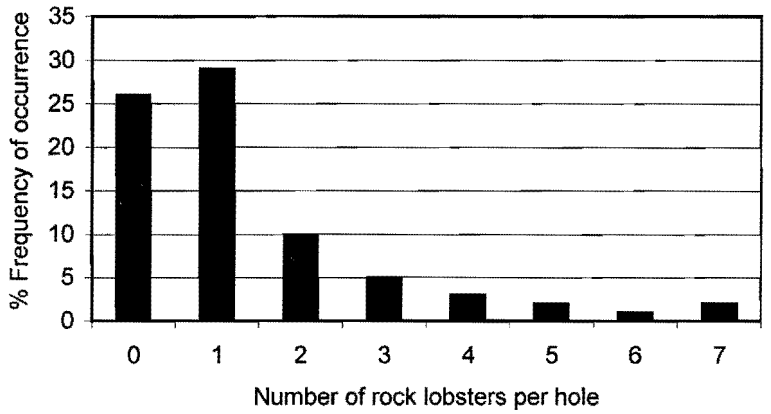

Fig. 4.11: Frequency of rock-lobster numbers occurring in 14 observed holes over 7 months.

4.3.5 Population monitoring

Between 80 % and 100 % of rock lobsters occurring in the reserve and non-reserve sites were of medium size. Less than 20 % comprised small or large rock lobsters. Data from the reserve site collected during the closed fishing season (May to October) were tested for homogeneity using the heterogeneity chi-square analysis and because they were found to be homogeneous (χ^2 = 3.38, d.f. = 2, $p > 0.05$, Zar 1984), they could be pooled. Data collected during the open fishing season (February to March and November to January) were similarly found to be homogeneous ($\chi^2 = 2.03$, d.f. = 3, $p > 0.05$) and pooled. Data from the non-reserve site for the open and closed season were also homogenous ($\chi^2 = 7.92$, d.f. = 4, $p > 0.05$, $\chi^2 = 0.7$, d.f. = 3, $p > 0.05$ respectively) and were pooled for each of the seasons. A 2 x 2 Chi-square (χ^2) contingency table was applied to the four sets of pooled data to test the null hypothesis that there was no difference in numbers of large rock lobsters occurring during the open and closed season in the reserve and non-reserve sites. Applying Yates' correction for continuity (Zar 1984), there was a significantly greater difference in numbers of large rock lobsters occurring between reserve and non-reserve sites, in both the open and closed fishing seasons ($\chi_c^2 = 6.42$, d.f. = 1, $p < 0.05$), thus rejecting the null hypothesis. Graphically it can be seen that more large rock lobsters were found within the reserve site, Alikreuk House, than outside the reserve throughout the sampling period (Fig. 4.12).

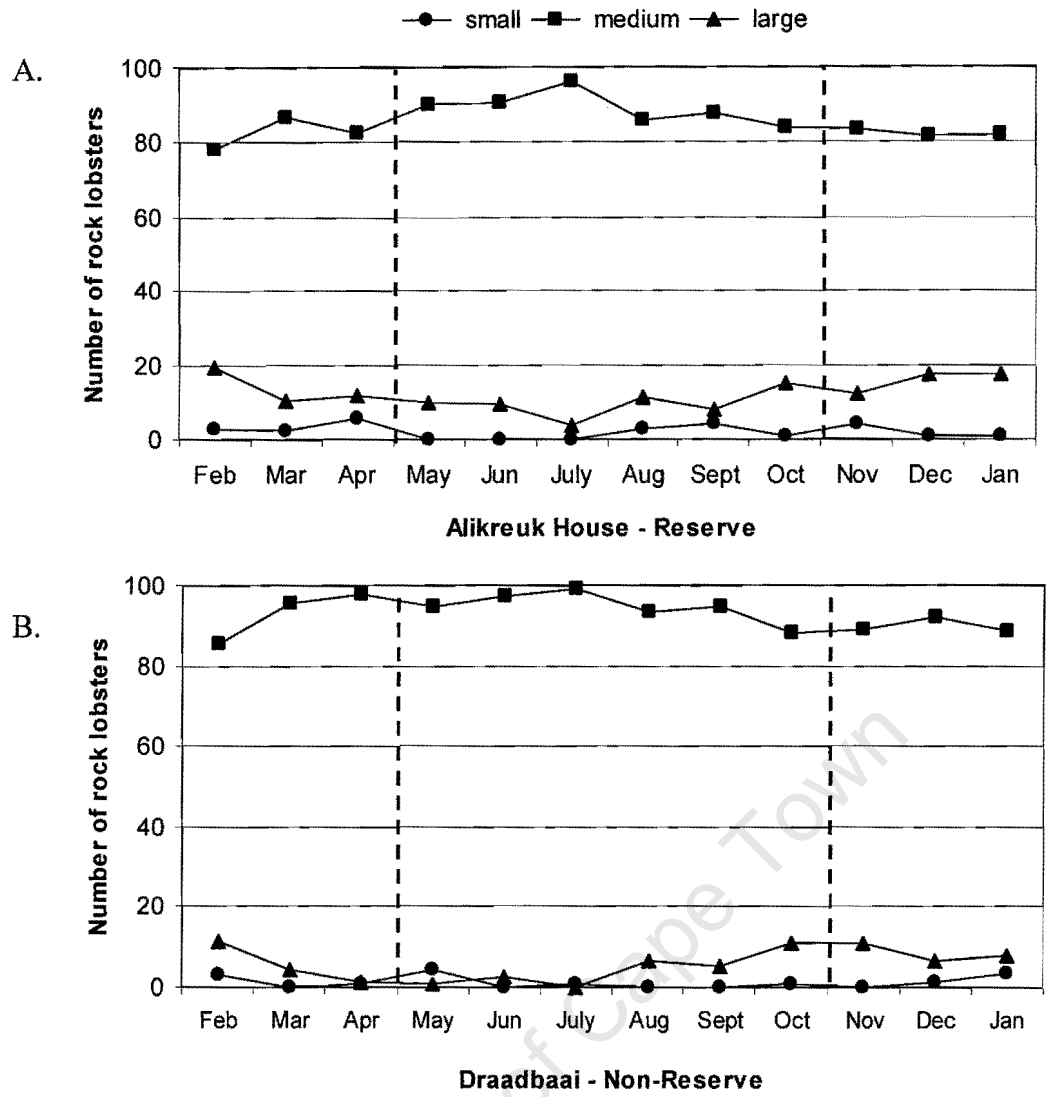

Fig. 4.12: Numbers of small (<40 mm CL), medium (41 – 80 mm CL) and large (>80 mm CL) rock lobsters occurring at the reserve site (Alikreuk House - A) and non-reserve site (Draadbaai - B) from February 2000 to January 2001. Dashed lines represent opening of the recreational fishing season (November) and close of the recreational fishing season (April).

The relative abundance (CPUE) of male rock lobsters in the reserve (sampled at Alikreuk House) was initially slightly higher than that of females (Fig. 4.13 A), except in July and August, just after the first substantial winter storms of the season, when females were more abundant. In October, males again became more abundant in the reserve site. Outside the reserve at Draadbaai, female rock lobsters were more abundant than males from March to September (with June being an exception), but from October onwards the CPUE had reversed and males were more abundant (Fig. 4.13 B). The overall abundance of rock lobsters was similar at both the reserve and non-reserve sites, with a peak in July-August and a steep decrease in CPUE in May. This decrease may relate to poor weather conditions experienced during sampling and is not a true reflection of the abundance in the area at the time. The onset of the first severe winter storms (July) coincided with the first appearance of ovigerous females at both sites (Fig. 4.13). By October (late spring), most ovigerous females had released their larvae and males were again in greater abundance at both sites (Fig. 4.13).

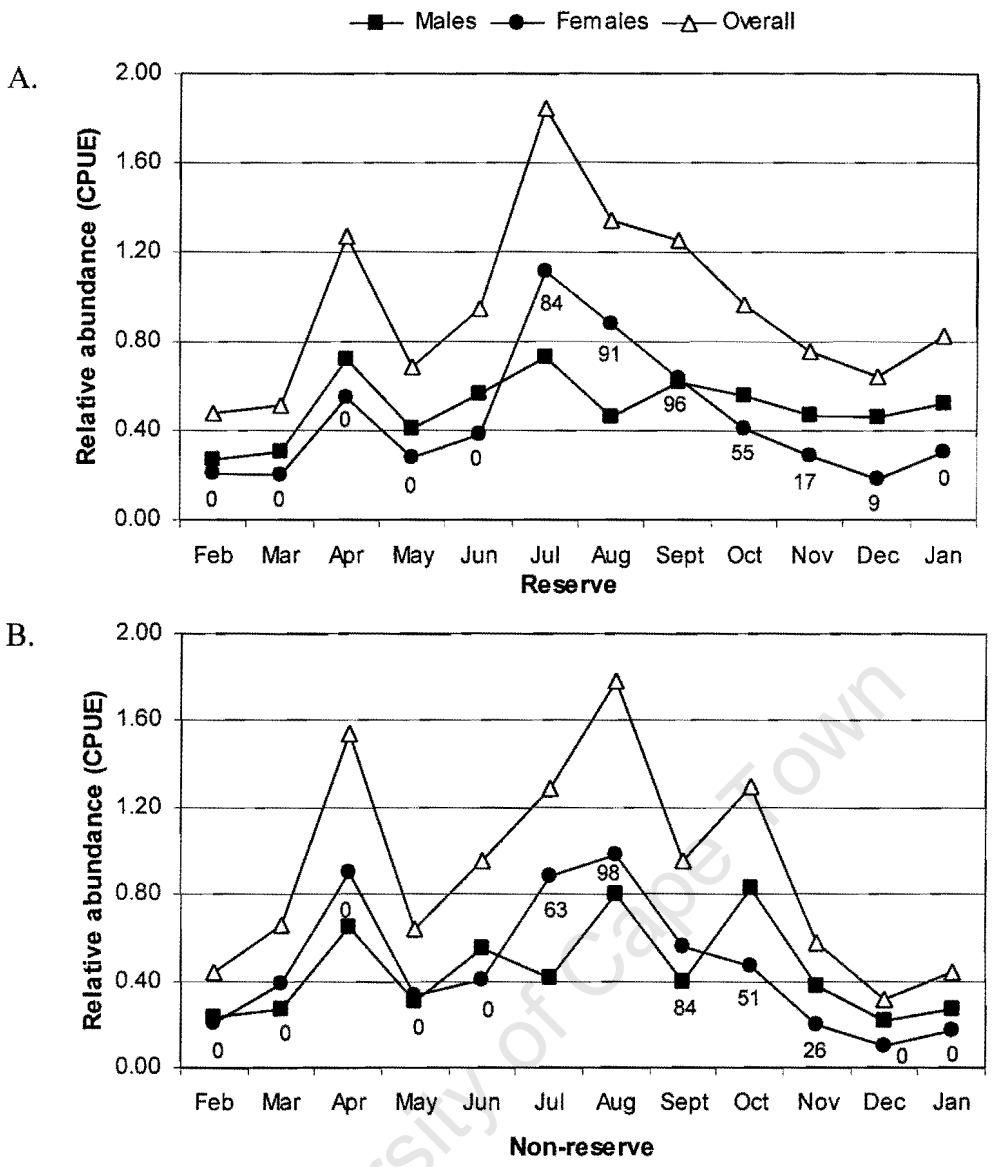

Fig. 4.13: Relative abundance (CPUE) of male and female rock lobsters at reserve (Alikreuk House - A) and non-reserve (Draadbaai - B) sites, sampled monthly from February 2000 to January 2001. The values below the data for females indicate the percentages of females that were ovigerous.

4.4 Discussion

4.4.1 Monitoring sizes and activities

My results suggested seasonal inshore-offshore movements of rock lobsters which appeared to be associated with moult cycles. Male and female rock lobsters, having different seasonal moult cycles, would be expected to undergo inshore movements at different times of the year, implying that the abundance and sex ratios will fluctuate through the seasons. At the Stony Point reserve however, there were no significant seasonal trends in small, medium or large rock-lobster abundance during the 12-month survey (Fig. 4.4). The low numbers observed during May are attributable to poor sampling conditions. A decline in numbers did occur from August to September, and similar declines were observed at other sites in this study (Alikreuk House and Draadbaai, Fig. 4.13). This is probably due to females moving offshore during this period, after their earlier influx inshore during June and July. Inshore-offshore movements of female rock lobsters are more clearly suggested by the data collected on the rock-lobster populations in both the reserve (Alikreuk House) and non-reserve (Draadbaai) study sites, which are discussed below.

Lobsters of all three size classes spent most of their time in shelters (Fig. 4.5). Large rock lobsters (> 80 mm CL) were more frequently observed out of holes and feeding than small rock lobsters (< 40 mm CL), which were hardly ever observed feeding (Fig. 4.5). These findings may be biased by the effects of diver disturbance, leading to an underestimation of the amount of foraging actually occurring.

4.4.2 Dietary study

Algae were the most abundant prey item found in the rock-lobsters diet from both sites, with the diet of rock lobsters at Stony Point consisting of up to 65 % algae. The percentage of algae found in the diet of rock lobsters occurring at Stony Point was almost identical to that found in rock lobsters held under conditions of intense predation threat in the mesocosm aquarium experiment, (see Chapter 3 and Fig. 3.6) Algae also dominated the diet of rock lobsters at Alikreuk House. In Chapter 3, it was concluded that the high algal component of the diet was due to the lobsters remaining in shelters where they had access to little else apart from algae. However at Stony Point and Alikreuk House, it is unlikely that the predation levels were sufficiently high to prevent foraging. Indeed, lobsters were observed feeding out in the open,

away from shelters. It is more likely that the high proportion of algae in the diets of rock lobsters there is due to a scarcity of their more usual prey (Mayfield & Branch 2000).

There was no significant difference in the gut-fullness indices between rock lobsters foraging at Stony Point and Alikreuk House. This suggests that rock lobsters at the two sites were foraging equally successfully, although consuming different prey items (Fig. 4.6).

Analyses of diet for rock lobsters of the same size class on the West Coast have yielded gut-fullness indices of 55.5 % (Mayfield *et al.* 2000) substantially greater than the figure of 28 – 39 % recorded here. Mayfield *et al.* (2000a) showed the diet of rock lobsters occurring on the West Coast of South Africa never contained foliar algae and predominantly comprised ribbed mussels (*Aulacomya ater*), black mussels (*Choromytilus meridionalis*), sea urchins (*Parechinus angulosus*), barnacles (*Notomegabalanus algicola*) and encrusting coralline algae. Other dietary surveys of *J. lalandii* have yielded similar results (Zoutendyk 1988; Barkai *et al.* 1996). These prey items made up little, if any, of the diet of rock lobsters at Stony Point and Alikreuk House. Mayfield and Branch (2000) showed that in the area where I worked, both sea urchin and winkles (*Turbo cidaris*) occurred at very low standing stocks in 1997, compared to surveys in 1980 (Field *et al.* 1980). Tarr *et al.* (1996) showed the abundance of both sea urchins and juvenile abalone (*Haliotis midae*) has decreased in the area since 1994. All of these studies further support the hypothesis that rock lobsters in this area forage largely on algae due to the low occurrence of more normal prey items.

4.4.3 Field tagging and monitoring

The tagging method employed is useful for short-term monitoring of individual rock lobsters within a defined and relatively small area. Monitoring individual, antennally-tagged rock lobsters over an 8-month period showed that rock lobsters displayed no hole fidelity, and little or no site fidelity. The most obvious feature emerging from monitoring the tagged lobsters was that relatively high rates of disappearance of tagged animals occurred. In all cases, the percentage re-sightings of tagged rock lobsters decreased over the period they were monitored. Several factors may have contributed to the decrease in re-sightings. Mortality, tag loss due to shedding or moulting, tagged lobsters being overlooked, or tagged lobsters moving out of the area are the most apparent possible explanations. Natural mortality of rock lobsters (*Jasus lalandii*) has been estimated to be less than 10 % per year (Johnston & Bergh 1993). Mortality of tagged rock lobsters was shown to be zero in laboratory studies conducted, thus eliminating natural rock-lobster mortality and tag-induced mortality as explanations for the rate at which re-sightings

decreased in the field. The possibility of rock lobsters losing their tags is also unlikely, as laboratory studies showed 100 % tag retention over eight weeks, excluding ecdysis, when the tags were shed. The possibility does exist that tag retention is lower in the field than in laboratory studies. However, the rock lobsters I tracked acoustically, for periods of up to 32 days, were also fitted with antennal tags, and none lost their antennal tags (see Chapter 6). Tag loss can thus be eliminated as a primary cause for the decrease in re-sightings of tagged rock lobsters. A single diver conducted all of the monthly 200-m^2 searches for tagged rock lobsters and was very familiar with the area, spending an equal amount of effort on each search. The possibility of overlooking tagged lobsters that were present during the searches was low and even if a small number of tagged individuals were overlooked, this is still unlikely to contribute extensively to the steep decrease of re-sightings. Dispersion of tagged rock lobsters out of the immediate area is thus the most likely explanation for the observed decrease in the percentage of tagged rock lobsters being re-sighted. If rock lobsters simply dispersed over a larger area than that searched, then their home range must be greater than 1250 m^2, i.e. the area covered by the entire grid, which was searched monthly. The possibility that movement out of the monitored site was not enhanced by disturbance associated with the tagging procedure cannot be disregarded. The underwater tagging used in the later part of my observations appeared to reduce disturbance, but may still have had an effect on emigration (Jernakoff 1987; MacDiarmid *et al.* 1991).

Rock lobsters showed no fidelity to specific holes within the blocks searched, with only 2.3 % of them ever being found in the same hole in consecutive months. The lobsters did not show any fidelity to the general area of the site searched. The data do not allow me to dismiss the possibility that *J. lalandii* displays site fidelity, but if it does exist, it was not evident at the scale of the area surveyed (200 m^2). The monthly searches of the larger 1250 m^2 area within which the 200 m^2 was embedded, also failed to detect more than a few tagged lobsters. It is thus likely that they dispersed beyond these larger boundaries as well. Furthermore, the distances rock lobsters moved between monthly sightings (Fig. 4.10) would soon have dispersed them out of the 200-m^2 area. The most likely interpretation of the disappearance of tagged lobsters is that *J. lalandii* does not display site fidelity. The fourteen rock-lobster holes that were monitored over seven months were most frequently vacant or occupied by single rock lobsters. However, the regular occurrence of between two and seven lobsters occupying one hole, with no aggressive displays towards each other, suggests that these rock lobsters are not territorial and readily share shelters with conspecifics. Two or more lobsters were found sharing holes during each month of observation (March to September) and no seasonal trend in shelter-sharing was apparent. The

possibility that territoriality occurs during the months that were not monitored (October to February) warrants further research.

4.4.4 Population monitoring

Recreational rock-lobster fishing is popular along the South-Western Cape and targets animals larger than the recreational legal size limit of 80 mm CL. I thus expected to find more large rock lobsters (> 80 mm CL) at Alikreuk House, which lies in the H. F. Verwoerd Marine Reserve, than at Draadbaai, a sheltered bay close by, but outside the reserve. This was indeed the case, as there was a significant difference in large rock-lobster proportions between the reserve and non-reserve in the open and closed fishing seasons. The difference was more obvious shortly after the open season began in November (Fig. 4.12).

Initially, male rock lobsters were more abundant at both sites, but in July, females became more abundant, remaining so until after September. This increased abundance of females occurred at the same time that the females became ovigerous, as well as the onset of winter storms (Fig. 4.13). The abundance of males appeared to remain stable, while the abundance of females increased in July. This increase would have been shortly after females moulted and many were, by then, ovigerous. Annual monitoring at both the reserve and non-reserve sites suggested that once females had moulted, they moved inshore to more protected bay areas for a period of approximately three months, after which the eggs were ready for release and the inshore abundance of females then decreased. This seasonal pattern was observed at both the reserve and non-reserve sites, but additional monitoring and long-term data would further elucidate the occurrence and timing of any seasonal inshore–offshore movement of female rock lobsters.

Many spiny lobster species have shown large-scale, longshore movements, often against the prevailing currents, to redress larval displacement, such as *Panulirus cygnus* (Herrnkind 1980), *Panulirus ornatus* (Moore & MacFarlane 1984), *Palinurus delagoae* (Groeneveld in press), *Palinurus gilchristi* (Groeneveld & Branch in press). Several *Jasus* spp. are also known to undergo regular large-scale migrations, often seasonally and onshore-offshore, e.g., *J. verreauxi* (Booth 1984), *J. edwardsii* (Annala 1981; McKoy 1983; Annala & Bycroft 1993), *J. frontalis* (Booth 1997). The only seasonal migration patterns thus far detected for *J. lalandii* have been strongly associated with low-oxygen water (Newman & Pollock 1971; Tomalin 1993; Noli & Grobler 1998).

Newman and Pollock (1971) monitored the movements of *Jasus lalandii* at Elands Bay on the West Coast of South Africa in the 1968–1969 fishing season. By monitoring the commercial catch and using diver counts, they ascertained a seasonal inshore–offshore movement pattern with males moving inshore during the summer months to moult in protected bays. Noli and Grobler (1998) and Tomalin (1993) also recorded inshore movement of *Jasus lalandii* during the summer months. All these studies have, however, associated the inshore movement during summer with the occurrence of low-oxygen waters offshore. In an attempt to escape the low oxygen, rock lobsters move inshore. No previous studies have monitored the seasonal movements of rock lobsters under normal sea conditions, i.e., in areas that do not experience low-oxygen events. My study took place in an area where no low-oxygen events have ever been recorded, and established that at two sites, one protected from fishing and the other not protected, female rock lobsters became more abundant inshore during winter months, once they were carrying eggs. The females remained proportionally abundant inshore until the onset of spring, when their numbers declined. This is presumably because they moved offshore, to release their eggs in deeper water. During this time, the inshore abundance of male rock lobsters at the two sites remained stable. These data suggest that in the area where I worked, female rock lobsters migrate seasonally inshore (in winter months), not males, as has previously been documented in other areas.

This seasonal study on movements of rock lobsters at Betty's Bay, east of Cape Hangklip generates alternative hypotheses regarding the movement patterns occurring in the area, compared to those originally proposed by Newman and Pollock (1971), Tomalin (1993) and Noli and Grobler (1998) of seasonal movements in response to low-oxygen events. Contrary to the findings of these studies, I believe the seasonal movement patterns observed at Betty's Bay are linked to intrinsic behavioural cycles. It also appears that rock lobsters displayed no site fidelity, at least at the scale of the site examined here (1250 m^2), and there was no evidence of fidelity to specific holes. Some of the rock lobsters did remain in the area for up to seven months. However most lobsters that were monitored exhibited wandering movements, with no clear start or end point, defined by Herrnkind (1980) as nomadism. The apparent scarcity of favoured prey items might induce rock lobsters to seek food over a large area, so that if home ranges exist, they may need to be large.

Studies on the effectiveness of marine reserves in South Africa have been confined largely to fish (Buxton & Smale 1989; Bennett & Attwood 1991; Attwood & Bennett 1994). There has been little documentation of the status of other species before and after declaration of marine

reserves, and it is thus difficult to surmise about their overall effectiveness. This study monitored two sites that lie in close proximity, one being within a marine reserve and the other, not. To a certain degree it did show that the marine reserve maintains a higher abundance of large lobsters relative to that outside. Before the start of the recreational fishing season (which opens in November) the abundances of rock lobsters at both sites were at similar levels (Fig. 4.13), however, shortly after the recreational fishing season started, the abundance of large rock lobsters declined at the non-reserve site whilst remaining stable at the reserve site. Indeed, a log-likelihood, goodness of fit test showed there to be a difference in the numbers of large rock lobsters occurring at the reserve and non-reserve sites, between open and closed seasons. This difference was, however, overshadowed by seasonal shifts in abundance evident at both sites. Large rock lobsters were more frequently observed at the reserve site (Fig. 4.12) suggesting that the reserve site offers protection for larger rock lobsters. Studies in marine reserves elsewhere in the world have yielded similar results (MacDiarmid & Breen 1992; Babcock *et al.* 1999; Edgar & Barrett 1999; Kelly *et al.* 2000), with rock lobsters being larger and more abundant inside reserves compared to fished areas adjacent to reserves. My results cannot be used to draw general conclusions that protected areas in South Africa will necessarily lead to an increase in the density of large rock lobsters. However, an intensive two-year survey conducted by Mayfield *et al.* (in press) on the effects of marine reserves on the fishery for *J. lalandii*, has shown that three rock-lobster sanctuaries situated on the West Coast of South Africa fail to yield higher rock-lobster catches than nearby fished areas. The size of rock lobsters captured in rock-lobster sanctuaries were not generally larger than those from fished areas and females do not produce greater numbers of eggs within the reserves compared to outside (Mayfield *et al.* in press). Mayfield *et al.* (in press) did, however, also survey the Betty's Bay marine reserve and here, rock-lobster abundance and fecundity were higher in the reserve than in nearby fished areas. The results from this study in the Betty's Bay area thus re-enforce the observations of Mayfield *et al.* (in press) from this area. The seasonal onshore-offshore movement of rock lobsters clearly demonstrated in this study and the large area over which rock lobsters appear to move does, however, undermine the value of small marine reserves or protected areas as a means of conserving this species.

The reserve site showed a higher abundance of large rock lobsters during both the open and closed fishing seasons, compared to the non-reserve site. The seasonal inshore movement of ovigerous females during winter months was apparent at both the reserve and non-reserve sites. Further long-term data sets are, however, needed to test the generality of the proposed seasonal movement patterns.

Advances in modern technology during the last decade have modernised methods of monitoring mobile marine species. Acoustic tracking has become a popular method of monitoring the movement of decapod crustaceans (Wolcott & Hines 1990; Collins & Jensen 1992; Newland & Chapman 1993; van der Meeren 1997; Cote *et al.* 1998; Kelly 1999). Although there is a large market from which to select the type of acoustic tracking devices employed, consideration must be given to the size and behaviour of the organism being tracked. It is vitally important to ensure that the size and weight of the transmitter does not impede the natural movements and behaviour of the organism (Anderka & Angehrn 1992).

Monitoring the movements of rock lobsters at Betty's Bay was thus continued by way of a pilot study using acoustic tracking (Chapter 6). Before this could be applied in the field, however, laboratory experiments were conducted to ensure that the selected acoustic transmitter had no effect on the movement and behaviour of *Jasus lalandii*. This forms the subject of Chapter 5.

Chapter 5

Small-scale laboratory studies of movements of the rock lobster *Jasus lalandii*: testing the effect of acoustic transmitters and access to shelter.

5.1 Introduction

With advances in modern technology during the last decade, it is becoming more popular to monitor individual decapod crustaceans by means of acoustic tracking (Wolcott & Hines 1990; Collins & Jensen 1992; Newland & Chapman 1993; van der Meeren 1997; Cote *et al.* 1998; Kelly 1999). It was previously not possible to utilize this form of tracking for many species, as the minimum transmitter size was considered too large for them to carry. However transmitter size has since decreased and accuracy of tracking has increased, making acoustic tracking an attractive method for monitoring movement of a wide range of species. An additional advantage of acoustically tracking mobile species is that data are available in real time and an almost unlimited number of data points may be collected. Previous monitoring of lobster movements relied on the recapture and returns of tagged animals (Chapter 2), which provided only two data points, one at release and one at recapture (Kelly 1999).

Acoustic tracking permits monitoring the movements of individual rock lobsters for as long as the transmitter is active. Transmitter life is however limited. The longer the transmitter life, the greater the battery size and the mass of the transmitter attached to the rock lobster. In compromising on length of battery-life, transmitters that are sufficiently small and light-weight to be attached to even relatively small species of rock lobster (e.g. *Jasus lalandii*) have been developed. Technology has also allowed acoustic transmitters to be developed with a replaceable battery option, which increases the life of the transmitter. Anderka and Angehrn (1992) note that, ideally, the transmitter and its attachment must not impede the normal behaviour of the tagged animal. This will not only ensure typical behaviour of the animal but will also allow comparable data to be gathered from tagged and non-tagged individuals. Caccamise and Hedin (1985) advocate that the maximum package weight added to the animal to be no more than 3 % to 5 % of the body weight, although it has been suggested that some small animals can carry transmitters that exceed the 5 % limit (Anderka & Angehrn 1992).

Acoustic transmitters can often be inserted into the body cavity of fishes, reducing the impact of increased drag on their swimming behaviour (Newland & Chapman 1993). In crustaceans, acoustic transmitters are usually externally attached to the carapace (Wolcott & Hines 1990;

Collins & Jensen 1992; van der Meeren 1997) and are shed when the animal undergoes ecdysis. The external attachment of a transmitter may induce a change in behaviour, inhibiting feeding or movement.

Smith *et al.* (2000) stipulate that to ensure acoustic tracking is yielding valid results, experiments with tagged and untagged individuals are necessary to test whether the acoustic transmitter has adverse effects on mobility and behaviour. This chapter primarily investigates the effects of acoustic transmitters on the rock lobster *Jasus lalandii,* by comparing the behaviour of tagged *vs.* non-tagged individuals under laboratory conditions. The acoustic transmitter tested was a VEMCO V8-2LR transmitter (see Table 5.1 for dimensions). The transmitters weighed well below the suggested 3 % to 5 % of body weight and were expected to have minimal, if any, effect on the rock lobsters. Nevertheless, it was important to establish that they do not hinder the movements of rock lobsters, prior to using the transmitters under field conditions. In aquarium experiments I tested acoustic transmitters under three conditions: in the absence of rock-lobster food; in the presence of food placed on the floor in the aquaria; and when food was placed on a raised platform (testing the influence of transmitters on climbing ability). I hypothesised that the acoustic transmitter would have no effect on the distances travelled over a fixed time period (rate), the speed or the foraging behaviour of the rock lobsters.

Concurrently I used these tests as an opportunity to examine the movements of rock lobsters in the presence and absence of food, and in relation to their distances from shelters. The importance of shelter selection by rock lobsters has been outlined in Chapter 3. Briefly though, it has been established that most species of rock lobsters prefer horizontal shelters with opaque covers and multiple openings (Spanier 1994) and do not always choose to reside in shelters with the largest dimensions (Zimmer-Faust & Spanier 1987). Spiny lobsters do select shelters that are large enough to be cohabitated by conspecifics and are generally gregarious (Zimmer-Faust & Spanier 1987).

My observations investigated the speed of movement and the amount of time *Jasus lalandii* spends near shelters relative to periods when it moves away from shelters. The observations were made in the absence of any predators and when food was either present or absent. I hypothesised that when there is no predation threat, rock lobsters will leave their shelters to forage whenever food is present. If no food was present, rock lobsters were expected to seek shelter or remain in the vicinity of shelters. Rock lobsters were also expected to move faster when they are away from protective shelters than when they are in their vicinity.

5.2 Methods

The experiments were conducted in the Marine and Coastal Management research aquarium. The tank used was circular, 3 m in diameter, with a water depth of approximately 0.6 m and had continuous seawater flow. Shelters, in the form of PVC pipes cut longitudinally in half, were provided in one half of the tank. These shelters had an opening at either end and were large enough for a single lobster to occupy. Two sizes of shelter were provided: eight large shelters (18 cm diameter, 22 cm length), and four small shelters (11 cm diameter, 22 cm length).

The acoustic transmitters tested were the VEMCO V8-2LR transmitters with replaceable batteries, the dimensions of which are shown in Table 5.1. and Fig. 5.1. Because of the expense of the genuine transmitters, artificial transmitters were constructed and used for experimental purposes. The artificial acoustic transmitters were moulded from a two-component composite epoxy adhesive to the same dimensions and weight as the genuine transmitters. The correct weight was achieved by adding small pieces of lead embedded into the epoxy before it hardened.

Table 5.1: Features of VEMCO-V8-2LR acoustic transmitters.

Transmitter	Length	Diameter	Weight of transmitter and battery	Weight of glue	Battery life
VEMCO-V8-2LR	50.9 mm	9 mm	6.4 grams	≈ 2 grams	36 ± 4 days

Sixteen male rock lobsters (*Jasus lalandii*) ranging in size from 85 – 97 mm CL were captured using hoop-nets and transported, under cool conditions, to the prepared tank. The imitation acoustic transmitters were attached to the carapaces of half of the rock lobsters using a fast-set glue gel (cyanoacrylate), while the remaining lobsters constituted controls. All the lobsters were then released into the experimental tank and allowed to acclimatize for seven days.

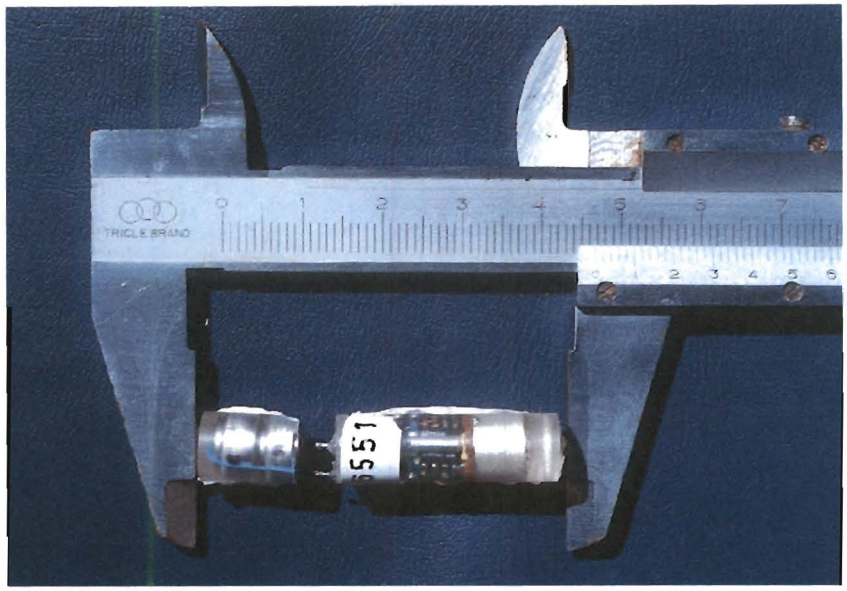

Fig. 5.1: The VEMCO-V8-2LR acoustic transmitter with replaceable battery (left) measured in millimeters against vernier calipers.

Experiment 1:

After the acclimatization period, rock lobsters were recorded from 18h00 to 19h00 using a horizontally mounted video camera. Sufficient light was provided using an infra-red light source, to ensure minimal disturbance to the lobsters (Priede 1992). The time of recordings coincided with the dusk peak in foraging activity, known for rock lobsters (Paterson 1969; Zoutendyk 1988)

Experiment 2:

Three days later, pilchard chunks were provided in a weighted mesh bag at the end of the tank furthest from shelters, and the movement of the lobsters again recorded from 18h00 to 19h00.

Experiment 3:

Two days thereafter, pilchard chunks were again provided in a similar area, except they were placed on top of a fiberglass rock, having dimensions of 40 cm high, 60 cm long and 50 cm wide. This was designed to test if the transmitters influenced the climbing ability of the lobsters. Observations were again made from 18h00 to 19h00.

All data were tested for normality using the Kolmogorov-Smirnov procedure and Levene's test for homogeneity. Where necessary, data were transformed using log + 1 for normality and homogeneity. The alpha value was set at 0.05 for all statistical analyses.

5.2.1 Distance analysis

The video-tapes from experiments 1, 2 and 3 were analysed by mapping the movement of each rock lobster onto a clear transparency, producing 16 movement tracings for each recording session (60 minutes). These tracings were electronically scanned and digitized into ArcView3 (ESRI) GIS software. The total distance each rock lobster moved in 60 minutes was calculated, and used to compare tagged *vs.* non-tagged animals within each of the three experiments by a fixed effects model, two-way ANOVA (StatSoft, Inc. 1995 STATISTICA for windows).

5.2.2 Area occupied

The position of each rock lobster was marked after every 5-minute interval during the one-hour recording session of experiments 1 and 2 only. The proportion of rock lobsters found in the one half of the tank (X = all the shelters) versus the other half (Y = no shelters) was compared between experiments 1 and 2 (Fig. 5.2). To eliminate any tank "edge-effect", (lobsters following the tank wall) a 50-cm border inside the tank edge was eliminated from this analysis. Any lobsters found in this area were excluded from the count and any subsequent analysis.

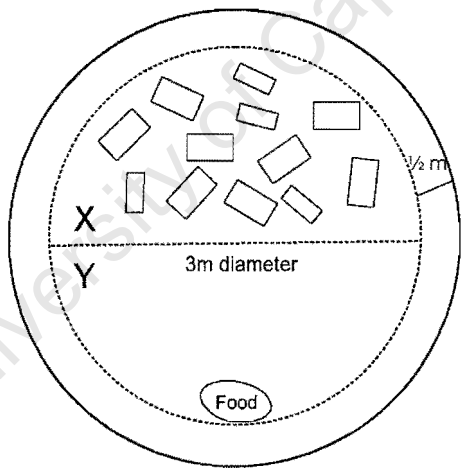

Fig. 5.2: Diagrammatic representation of experimental tank at M & CM aquarium indicating area X with shelters (indicated by rectangles) and area Y where food was placed during the second recording. The half-meter exclusion boundary is shown. Diagram not drawn to scale.

5.2.3 Rate of movement

The rate of movement was determined by measuring how far the lobsters moved in random 30-second intervals. During the recordings of experiments 1 and 2, lobsters in area X and area Y (Fig. 5.2) were randomly selected 24 times (12 in each area) and the distance moved in 30 seconds recorded. The average distance moved in 30 seconds (rate of movement) was determined and compared with and without food, near to and far from shelters. Log + 1

transformed data were tested using a two-way ANOVA with a 2 X 2 factorial design with food and shelter as fixed effects (StatSoft, Inc. 1995 STATISTICA for windows).

5.3 Results

5.3.1 Distance analysis

Fig. 5.3 shows the average distances moved in 60 minutes by tagged *vs.* non-tagged animals exposed to three different food conditions (without food, with benthic food or with raised food). A fixed effects model, two-way ANOVA showed a significant difference for the effect of the food factor, no significant difference for the transmitter factor and no significant interaction between food and transmitter (Table 5.2).

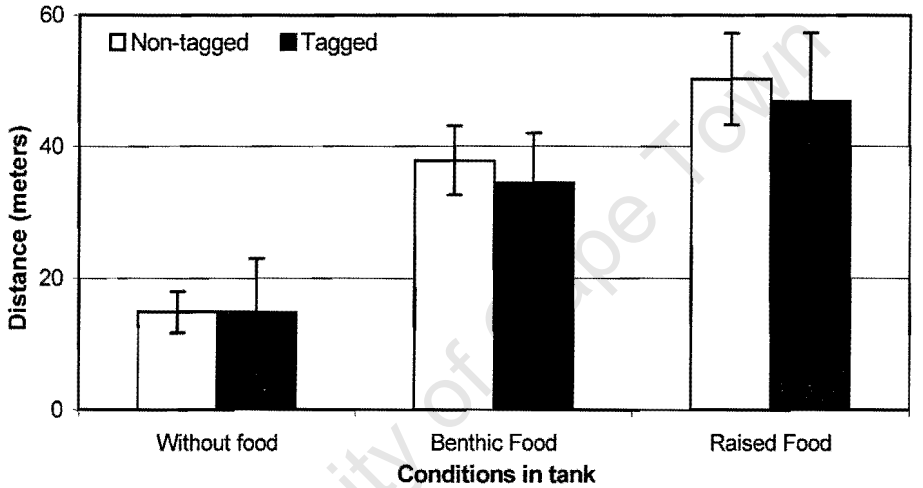

Fig. 5.3: Total distance moved per hour by rock lobsters without food, with benthic food or with food on a raised platform. Values are means ± 1 S.E. Dark = movement of tagged lobsters; Light = movement of non-tagged lobsters. (n=16)

Table 5.2: Results of two-way ANOVA with fixed effects between food conditions (3) and transmitter presence (2) (n=8) and post-hoc Tukey test to show significant differences between food conditions.

	Two-way ANOVA						
	df effect	MS effect	df error	MS error	F	p-level	
Food	2	52069888	42	4279391	12.16759	$\ll 0.001$	Significant
Transmitter	1	179218.64	42	4279391	0.041879	0.839	Not significant
Food x Transmitter	2	643988.19	42	4279391	0.150486	0.861	No interaction
	Post-Hoc Tukey test						
Without food *vs.* Benthic food			$p = 0.008$			Significant	
Without food *vs.* Raised food			$p \ll 0.001$			Significant	
Benthic food *vs.* Raised food			$p = 0.22$			Not significant	

A post-hoc Tukey test showed there to be a significant difference between lobsters without food *vs.* those with benthic food or raised food but no significant difference between lobsters with benthic food or raised food (Table 5.2. and Fig. 5.3)

5.3.2 Area occupied

The number of rock lobsters observed at each 5-minute interval varied due to the exclusion of lobsters found within the half-meter border. Fig. 5.4 illustrates the movements of rock lobsters between the two halves of the tank during the one-hour observation period (18:00 – 19:00). In the absence of food (Fig. 5.4 A) rock lobsters were seldom observed outside the area that contained shelters, and no more than two individuals were ever concurrently observed in the area without shelters, during any time interval. Throughout the time period an increasing number of rock lobsters were found near to shelters but there was no change in the number of lobsters found in the area lacking shelters. This implies that rock lobsters moved away from the wall (the 50-cm exclusion boundary) and towards the shelters.

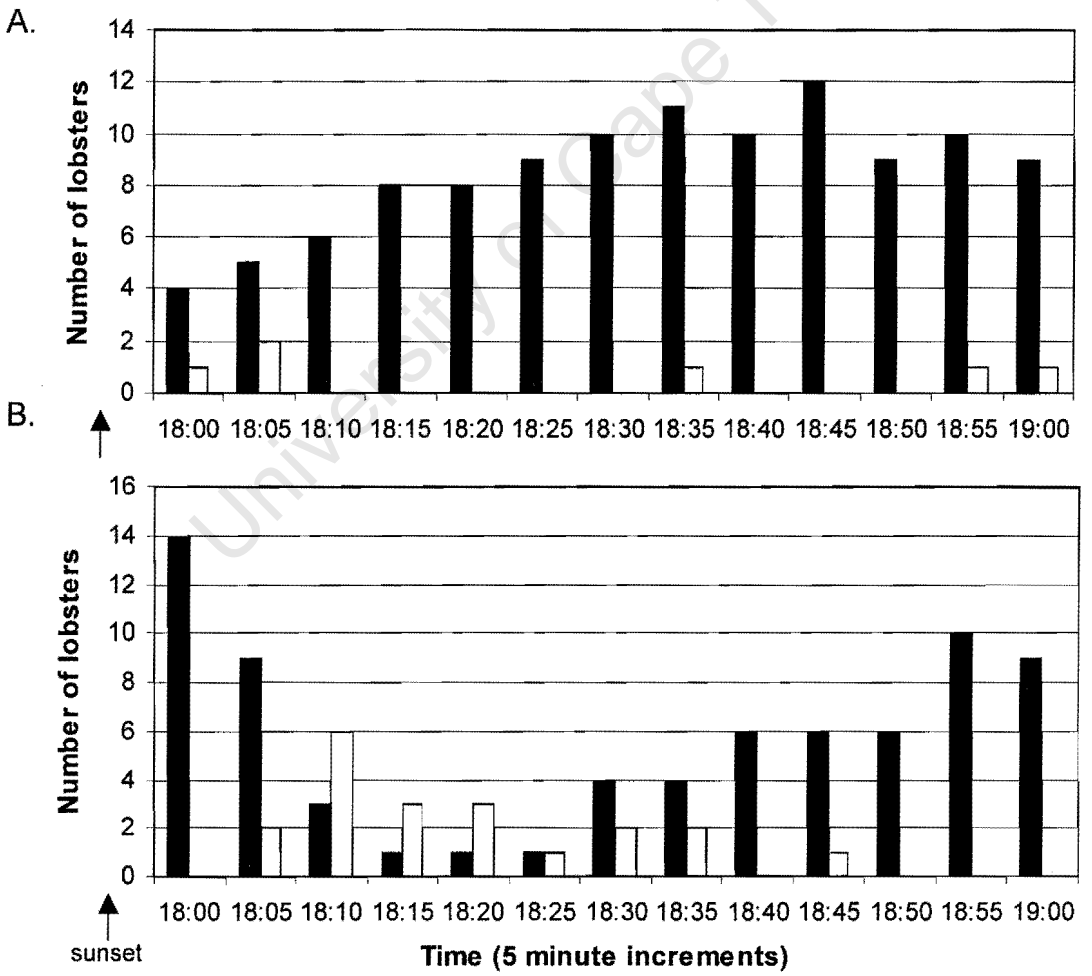

Fig. 5.4: Number of rock lobsters occurring in area X (the area of the tank containing shelters: shaded bars) *vs.* area Y (the area of the tank containing no shelters: clear bars) when food was absent (A) and when food was present (B), during a one-hour time series, monitored at 5 minute intervals. (n=16)

At the time food was added (Fig. 5.4 B) in the area opposite the shelters, at 18:00, the majority of rock lobsters were aggregated in or near shelters, with no rock lobsters being in area Y. Within 5 minutes, lobsters had begun moving towards the food source. Lobsters continued to move out of area X and into area Y for at least 20 minutes after the food was introduced. Although the numbers of rock lobsters moving out of X are not reflected as a corresponding increase in Y, this is explained by the fact that some lobsters were excluded from the count because they occurred in the 50 cm tank "edge effect" exclusion zone. After approximately 30 minutes of food presence, the number of rock lobsters found in the vicinity of shelters began to increase again. At the end of the hour of observation, the numbers found in this area were approaching those originally observed there and none were found in the area lacking shelters.

5.3.3 Rate of movement

The movement rate of rock lobsters was defined as the distance moved during a 30 second time period. Graphically (Fig. 5.5) it is evident that the rate of movement was much higher when the lobsters were positioned far from shelters. A fixed effects two-way ANOVA indicated a significant difference between the rate of movement near shelter *vs.* far from shelter ($F_{0.05,1,\ 44}$ = 87.93, $p \ll 0.001$) but no significant difference was detected whether food was present or absent ($F_{0.05,1,\ 44}$ = 1.56, p = 0.22) and there was no significant interaction between shelter and food presence ($F_{0.05,1,\ 44}$ = 0.12, p = 0.73). Rock lobsters moved at a slower rate when near the protection of their shelters and faster when in an exposed area.

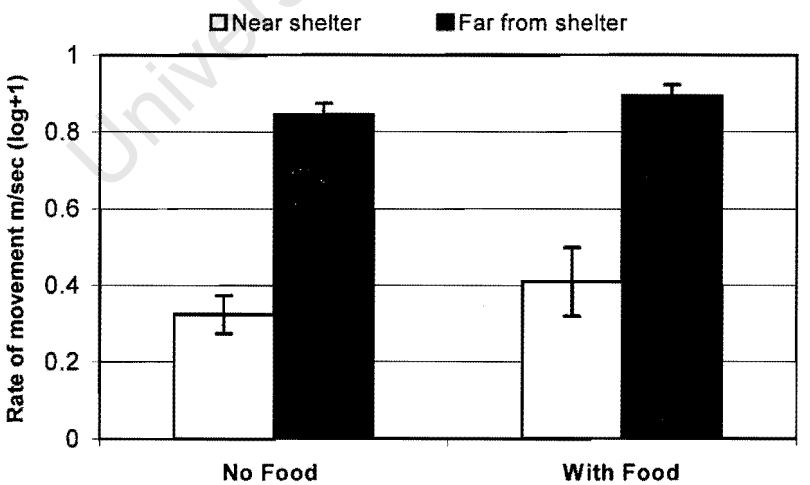

Fig. 5.5: Average distance moved during 30 seconds, near to shelter and far from shelter, with and without food. Values log + 1 transformed for normality and homogeneity. (n = 16)

5.4 Discussion

Acoustic tracking of cryptic animals such as decapod crustaceans can reveal valuable detailed information relating to their activities and movement over large spatial and temporal scales. The movements of rock lobsters have been closely studied using various acoustic means of tracking in Canada, Norway, New Zealand and the United States (O'Dor *et al.* 1998; Kelly 1999). Acoustic tracking can only be effective if the presence of the transmitter on the animal does not seriously impair its mobility and routine behaviour (Smith *et al.* 2000).

The experiments conducted in the laboratory aquarium found no statistical difference in the average distance moved between tagged and non-tagged *Jasus lalandii* irrespective of whether food was present or not (Table 5.2; Fig. 5.3). Although only one parameter of behaviour (distance moved over time) was tested, the ability to successfully forage and climb vertical structures was also examined. Personal observation of rock-lobster behaviour in the tank showed that there was no higher incidence of foraging by untagged rock lobsters. Tagged rock lobsters displayed speed and agility in moving, equivalent to that of untagged individuals. Ability to seek and take up shelter, to carry food, to climb both the artificial rock and a small ledge of the tank and to swim rapidly by means of tail-flip, did not appear to be any different for tagged and untagged rock lobsters. Tagged and untagged rock lobsters moved similar distances at similar rates and responded similarly to the presence or absence of food. Thus, VEMCO V8-2LR acoustic transmitters had no evident effect on the lobsters, and were considered suitable for the acoustic tracking of *Jasus lalandii*. This conclusion is, however, only valid for the size class examined in this study (> 85 mm CL). *Jasus lalandii* smaller than 85 mm CL would have to be further tested for their ability to carry these transmitters.

During electromagnetic tagging studies Jernakoff (1987) tested the effects of transmitters on *Panulirus cygnus*. Although the presence of transmitters did not appear to influence the behaviour of the lobsters, capture and handling accompanying the attachment of transmitters could have induced a response. Jernakoff (1987) observed that several lobsters disappeared within the first few nights after tagging and were not seen again. Extensive studies by MacDiarmid *et al.* (1991) on the effects of capture and tagging of *Jasus edwardsii* showed that capturing lobsters did not influence the total number of lobsters leaving the study site, but did increase the likelihood of lobsters moving away within the 24 hours following capture. In both studies, the rock lobsters were influenced by the disturbance of capture rather than the attachment of a transmitter (Jernakoff 1987; MacDiarmid *et al.* 1991). It is almost impossible to individually identify an adequate number of rock lobsters for movement studies without some

form of external markings. To mark lobsters, they have to be captured. Minimizing the negative effects of capture may reduce the amount of stress the animal is exposed to and, hence, decrease the amount of induced movement.

Rock lobsters seek shelter for protection from predators, to moult and to mate (Spanier 1994). They generally venture out of their shelters to forage. Nocturnal foraging is considered an anti-predatory mechanism and is widespread among crustaceans (Spanier & Zimmer-Faust 1988). My study was conducted in the absence of predators, yet it was evident that when no olfactory food stimulus was present to encourage foraging, lobsters rarely left the vicinity or protection of their shelters. However, when food was introduced, lobsters rapidly left the protection of their shelter, moved towards the food and either grabbed food and brought it back to consume near the shelters or proceeded to consume food in the area that lacked shelters. After about 30 minutes of foraging, most rock lobsters moved back towards the protection of the shelters (Fig. 5.4). Thus, rock lobsters sensed when the food was present and reacted immediately. When no food was present or when the lobsters had just fed, they mostly remained in or near to shelters, even though there was no risk of predation.

When examining the rate of movement, it was evident that movement was more rapid when the lobsters were further away from shelter. Their rate of movement when close to shelter was considerably less. This pattern of behaviour was almost identical whether food was present or absent (Fig. 5.5). These results suggest that rock lobsters were responding to a perceived increase in risk when far from the protection afforded by shelters. They moved faster, although there was no predatory threat. When food was introduced in the exposed area of the tank, the rock lobsters move rapidly towards the food, but once feeding was complete, or the lobsters had secured a piece of food, they moved back to shelter. Again, this behaviour was demonstrated even though no predators were present.

The findings from these experiments suggest that rock lobsters have a strong instinct and well-developed behaviour patterns. They seek shelter for protection, even when there is no threat, and move faster when away from the vicinity of shelter. Lima and Dill (1990) suggest that animals can assess the risk of predation and adapt behaviour patterns during their lifetime. In this instance however, the rock lobsters continued to forage in short bursts and seek shelter for most of their time despite the absence of predators. The experiment duration (including acclimatisation) only lasted 15 days. This period of time was possibly too short for the rock lobsters to have altered their natural behaviour to adjust to the lack of any predatory threat. In

Chapter 3, I demonstrated that in the Kelp Forest tank of the Two Oceans Aquarium in Cape Town, rock lobsters displayed extreme fidelity to shelters and rarely left them, even when food was placed within 1.5 m of the entrance to a shelter. I ascribed this behaviour to the extreme threat posed by large, predatory fish. It is difficult to make valid comparisons between that study and this one because there are many differences in the circumstances. Nevertheless, in the present study, where there was no predatory threat, rock lobsters responded immediately to food and left the area that provided shelter, to forage.

In summary, the findings of the laboratory aquarium experiments showed that:

- The acoustic transmitter tested (VEMCO-V8-2LR) had no apparent adverse effects on the behaviour of rock lobsters greater than 85 mm CL.
- Rock lobsters tended to remain in the vicinity of shelters unless food was introduced, and even then, they foraged rapidly and returned to shelters.
- The rate of movement was faster when lobsters left the area that contained shelters.
- These latter two responses occurred even though predators were absent.

Having established this, I progressed to further examine movement patterns of *Jasus lalandii* in their natural environment by using acoustic tracking in the field (Chapter 6).

Chapter 6

An acoustic tracking pilot study of *Jasus lalandii* movement patterns.

6.1 Introduction

A variety of techniques have been used to monitor the movement patterns of rock lobsters at both small and large scales. Tag and recapture is commonly used to detect large-scale movements (Annala 1981; McKoy 1983; Booth 1984; Moore & MacFarlane 1984; Campbell & Stasko 1986; Annala & Bycroft 1993; Chapter 2, this thesis). This technique often operates in conjunction with commercial fisheries and yields large-scale movements over long time-periods. Advantages and disadvantages relating to data gathered using this technique are referred to in Chapter 1. Visual monitoring of the movement patterns of tagged lobsters allows detection of smaller-scale movements within a pre-determined area (Ennis 1984a & b; MacDiarmid 1991; MacDiarmid *et al.* 1991; Chapter 3 & 4, this thesis). This method also has shortcomings (outlined in Chapter 1), the most obvious being the limited size of the area that can realistically be thoroughly searched. Because it is impractical to survey an entire population, the information gained using these methods is based on a sub-sample of the population. Sub-sampling from populations can often be misinterpreted and the population status either over- or under-estimated (Smith *et al.* 1998). However, these sampling methods provide valuable basic knowledge, which, by using further monitoring techniques, can be refined to yield a more definitive understanding of movement patterns.

Most marine decapods (including rock lobsters) are highly mobile, cryptic animals that are often most active during the early hours of the morning and evening (Paterson 1969; van der Meeren 1997; Smith *et al.* 1998). The habitat in which they exist is often inaccessible for accurate sampling (van der Meeren 1997) and innovative methods are frequently employed when assessing movement behaviour. The methods available to measure the movements of individuals on an appropriate scale are limited. With advances in technology, tracking methods have improved. Radio tracking can be used in terrestrial and freshwater environments, but radio energy is severely attenuated by seawater (Smith *et al.* 2000). Ultrasonic tracking, using a fixed hydrophone array, has proved unsuitable for mobile species inhabiting densely vegetated, rocky seabeds. Electromagnetic tracking relies on a uniform substratum upon which cables can be layed, and is thus unsuitable for tracking rock lobsters that inhabit rocky reefs (Smith *et al.*

2000). Acoustic telemetry has, thus far, proven to be the most suitable means of remote tracking for spiny lobsters (Cote *et al.* 1998).

Sound is a mechanical vibration that can only propagate through a medium (Priede 1992). The velocity of sound depends on the physical properties of the medium through which it is transmitted. Temperature, pressure and salinity determine the extent of refraction in water, so that sound does not always travel in straight lines (Priede 1992). This can produce "shadow zone" areas, where sounds cannot be detected, even though the receiver is in close proximity to the source. Background acoustic noise is expected to be high in coastal waters and the passage of sound from a transmitter can suffer attenuation due to shallow water, aquatic vegetation or turbid conditions (Stasko & Pincock 1977; Priede 1992). Absorption of sound increases with an increase in frequency (Hz). A popular frequency for tracking in coastal and freshwater is 75 Hz, for which the typical working range is up to 1 km (Preide 1992). The choice of frequency for tracking systems is a compromise between attenuation at high frequencies and noise at low frequencies.

The techniques employed to monitor the movements of a species generally reflect the questions being asked (Kelly 1999). Most studies are forced to compromise between the detail of information gained and the sample size. Studies yielding very detailed results are usually based on a relatively low sample number, whereas coarse movement patterns can be gained from large-scale tag-recapture programs (Chapter 2). Acoustic tracking yields detailed movement observations but is usually limited to a small sample size. The reason for this is predominantly the restricted frequency width, which limits the number of individuals that can be tracked simultaneously without confusion, and the expense of the emitters. The period of time the transmitter will be active before the battery life runs out, is another limitation on the amount of data that can be collected by acoustic tracking (see Chapter 5).

Several studies have, however, successfully utilised various means of remote tracking to monitor the movements of both clawed (van der Meeren 1997; Smith *et al.* 1998 & 2000) and spiny lobsters (Chapman *et al.* 1975; Herrnkind *et al.* 1975; Ramm 1980; Jernakoff *et al.* 1987; O'Dor & Webber 1991). The most successful study has been that conducted by Kelly (1999) who acoustically tracked the movements of 32 individual *Jasus edwardsii* for periods of up to one year, observing both male and female seasonal movement patterns.

My studies on the movement patterns of *Jasus lalandii* have thus far shown (1) no evidence of long-shore migration (Chapter 2), (2) that under intense predation threat, they displayed high levels of fidelity to shelters and moved very little (Chapter 3), (3) under field conditions they do not display fidelity to specific holes and showed no sign of having a home range smaller than 1250 m^2 (Chapter 4) and (4) they display seasonal onshore-offshore movements seemingly related to moult cycles (Chapter 4). Acoustic tracking has been identified as the most suitable means of tracking spiny lobsters (Cote *et al.* 1998). However, *Jasus lalandii* has thus far not been tracked using any form of telemetry. This is predominantly due to its comparatively small size, which precluded the attachment of transmitters that, until recently, have been large and heavy. With improving technology, smaller, light-weight transmitters have become available. It has already been shown in aquarium experiments that the acoustic transmitter selected for this study (VEMCO V8-2LR) had no adverse effects on the behaviour of *Jasus lalandii* larger than 85 mm CL (Chapter 5). Here, I describe an field-based pilot study that tested the suitability of the VEMCO V8-2LR acoustic transmitter for tracking *Jasus lalandii.* Acoustic tracking of the movements of *Jasus lalandii* can provide a link between the large-scale tag-recapture studies (Chapter 2) and small-scale behavioural studies (Chapter 3 and 4). The practicality of using acoustic transmitters to track *Jasus lalandii,* and detailed information on the movements of the individuals tracked, are reported in this chapter.

Due to the high cost of the transmitters and limits on the amount of time that could be devoted to tracking, the sample size of rock lobsters that were acoustically tracked was small. The main purpose of the study was to investigate the viability of the acoustic technique, rather than a long-term study detailing lobster movement. Nevertheless, the patterns revealed from this small sample size provided a qualitative insight into lobster movements and further expanded on observations made by following antennally-tagged rock lobsters in Chapter 3 and 4.

6.2 Methods

The study was divided into two sections: an initial investigation of the operating efficiency of acoustic transmitters in rocky areas with dense kelp beds and, subsequently, acoustically tracking the movements of a further three rock lobsters. To test the efficiency of the acoustic transmitter, a sheltered site with rocky reefs and dense kelp beds (*Ecklonia maxima*) was selected. Although the selected site, Maasbaai, lay outside the nearby H. F. Verwoerd marine reserve, the initial study was conducted whilst the fishing season was closed (June 2000) and the risk of the acoustically tagged rock lobster being fished out was low. All subsequent acoustic tracking was conducted inside the H. F. Verwoerd marine reserve at Betty's Bay in the South-Western Cape,

South Africa, during January and February 2001. This area has large tracts of rocky reef with dense kelp beds, interspersed with small patches of sand-flats, which is considered typical habitat of *Jasus lalandii*.

The movements of four male rock lobsters, ranging in size from 86 mm CL to 98 mm CL, were tracked for periods of up to 32 days. The transmitters used were VEMCO V8-2LR transmitters with replaceable batteries (see Chapter 5, Table 5.1 for specifications), which emit an individually coded acoustic signal between 65.5 and 76.8 kHz. Each rock lobster was also tagged with a colour-coded antennal tag (see Chapter 3, Fig. 3.1), to aid in identification of the lobsters with minimal disturbance, even when they were in shelters or crevices. A diver hand-captured each rock lobster and surfaced to a boat anchored nearby. The acoustic transmitters were attached to the dorsal surface of the carapace using a fast-set glue gel (cyanoacrylate) (Fig. 6.1). The glue was allowed to set for approximately five minutes after which the rock lobsters were returned to the area from which they were captured.

Fig. 6.1: VEMCO V8-2LR acoustic transmitter attached to the dorsal surface of a 90-mm CL male rock lobster. Note the colour-coded antennal tag attached to the left hand antennae.

Tracking was carried out, on average, every four days (S.E. = 0.37), from a small boat using a VR-60 ultrasonic receiver and V-10 hydrophones from VEMCO Ltd. The boat was manoeuvred to the position where the strongest signal was obtained from the surface, and a diver was deployed with a hand-held DPL-275A Datasonics Inc. pinger locator and the acoustically tagged rock lobster tracked underwater and visually located. The diver would then surface directly above the rock lobster, the boat would approach the diver and the Global Positioning System (GPS) of the diver was recorded. With the discontinuation of selective availability on all GPS's from 1 May 2000, the accuracy obtained by a GPS ranges between 7 m and 15 m. This thus set the accuracy of measurements of the positions of rock lobsters tracked in this study.

6.3 Results

The initial experiment, conducted at Maasbaai (Fig. 6.2), aimed at determining the effectiveness of the acoustic transmitter, yielded excellent results. The acoustically tagged rock lobster could be detected from a distance of about 100 m and, using the hand-held pinger locator, the exact location of the rock lobster could easily be identified. The signal penetrated through rock and dense kelp beds, allowing the rock lobster to be easily tracked, even when it was sheltering deep in a rock crevice. The gross distance moved by this 90-mm CL male rock lobster was 62 m over 15 days (Fig. 6.2). The rate of movement over this time period was 4.1 m/day. Due to the nature of the site, the rock lobster was always found at a depth of 8 m. Although the theoretical battery life of the transmitter used was 36 days ± 10 %, the rock lobster, with its acoustic transmitter, was removed after 15 days and monitored further in the laboratory to test the longevity of the battery. This particular battery remained active for 51 days, but from day 48, the signal started weakening until it had completely stopped by day 51.

Having used this lobster to test the practicality of using acoustic transmitters in the field and the probable maximum battery-life of the transmitters, acoustic transmitters were attached to three West Coast rock lobsters and released at Betty's Bay.

The first of these rock lobsters (90-mm CL male) yielded a gross movement of 522 m over 32 days, the average rate of movement being 16.3 m/day (Fig. 6.3). This rock lobster moved from one kelp bed, across a sand-flat area to another kelp bed where it remained until the transmitter was removed after 32 days. The initial movement across the sand-flat took place at a rate of 39 m/day whereas the remaining movements within the kelp had an average rate of movement of 7.2 m/day. The depth at which the rock lobster was located varied between 5 m and 17 m.

The second rock lobster (98-mm CL male) moved a total of 127 m over 22 days yielding a mean rate of movement of 5.8 m/day (Fig. 6.4). It remained within a depth zone of 5 m throughout the tracking period. After seven observations over 22 days, the rock lobster was not located again and although an area in excess of 2 km^2 surrounding the last known location of the individual was searched on three separate occasions, neither the lobster nor the transmitter were located.

The third transmitter was used to track the movements of an 86-mm CL male rock lobster. This individual moved 1146 m over 32 days averaging 35.8 m/day (Fig. 6.5). The greatest movements were observed during the first, third and fourth observation sessions when the rock

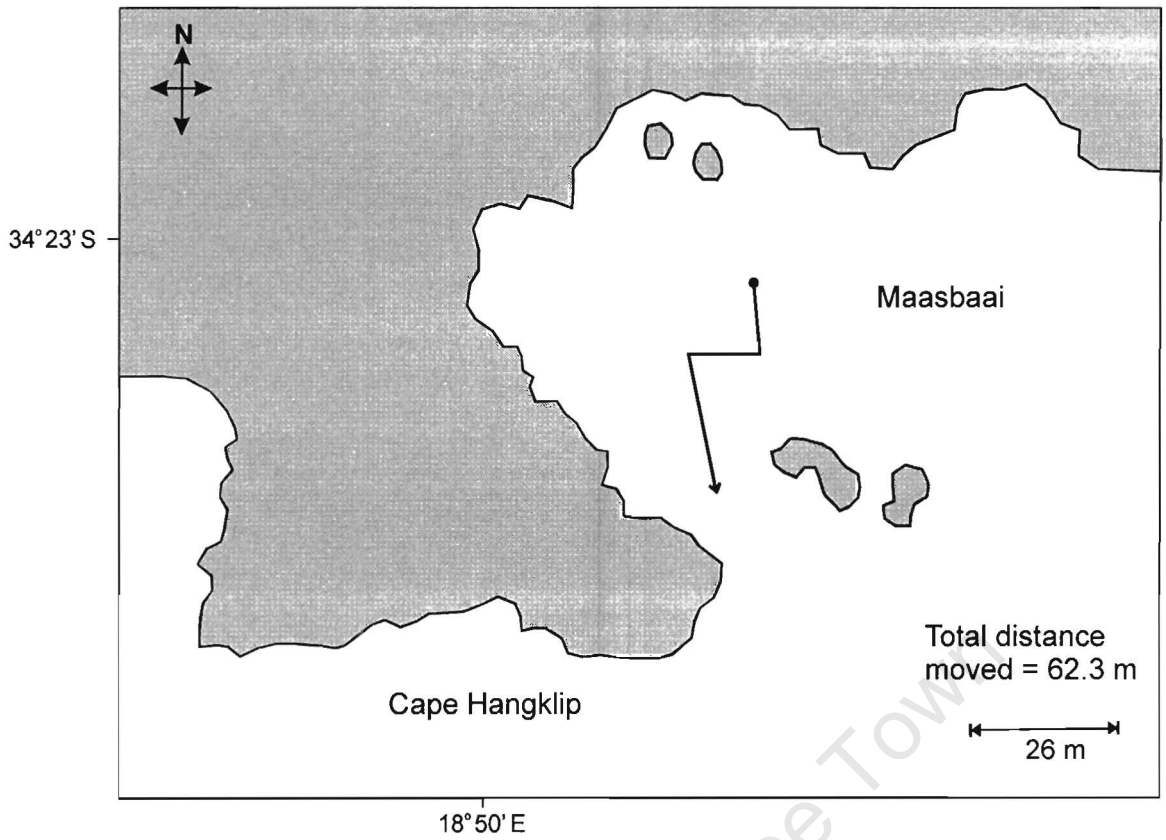

Fig. 6.2: Diagrammatic representation of movements of an acoustically tagged rock lobster (90-mm CL, male), tracked at Maasbaai on 5 occasions over 15 days.

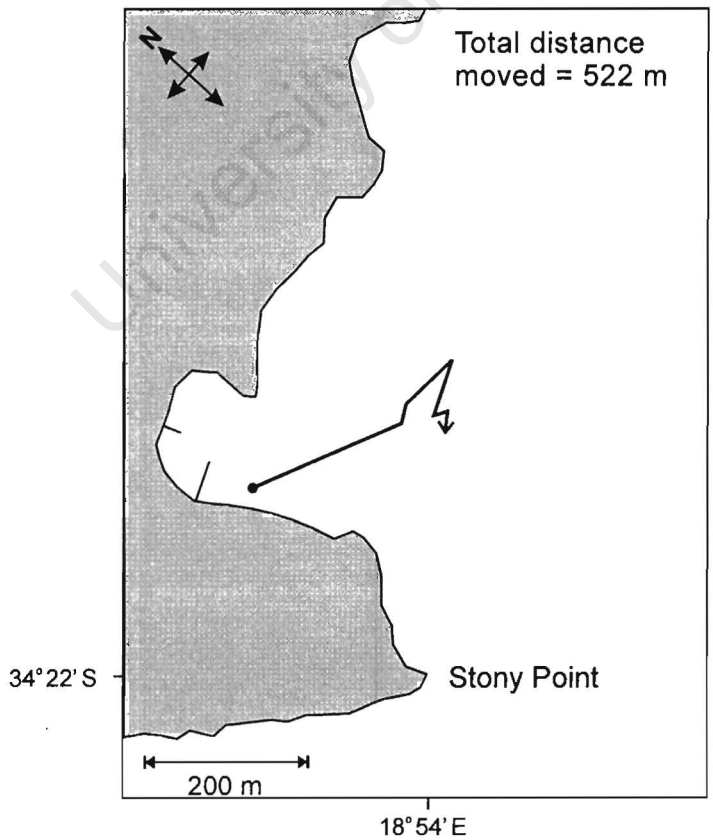

Fig. 6.3: Diagrammatic representation of movements of an acoustically tagged rock lobster (90-mm CL, male), tracked at Betty's Bay on 7 occasions over 32 days.

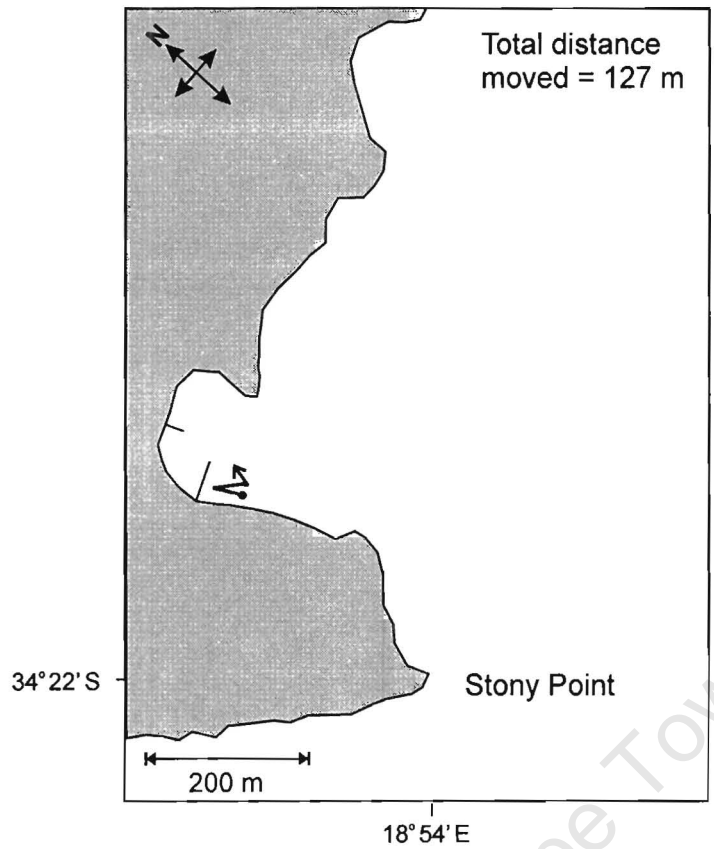

Fig. 6.4: Diagrammatic representation of movements of an acoustically tagged rock lobster (98-mm CL, male), tracked at Betty's Bay on 7 occasions over 22 days, after which the rock lobster and the transmitter were lost.

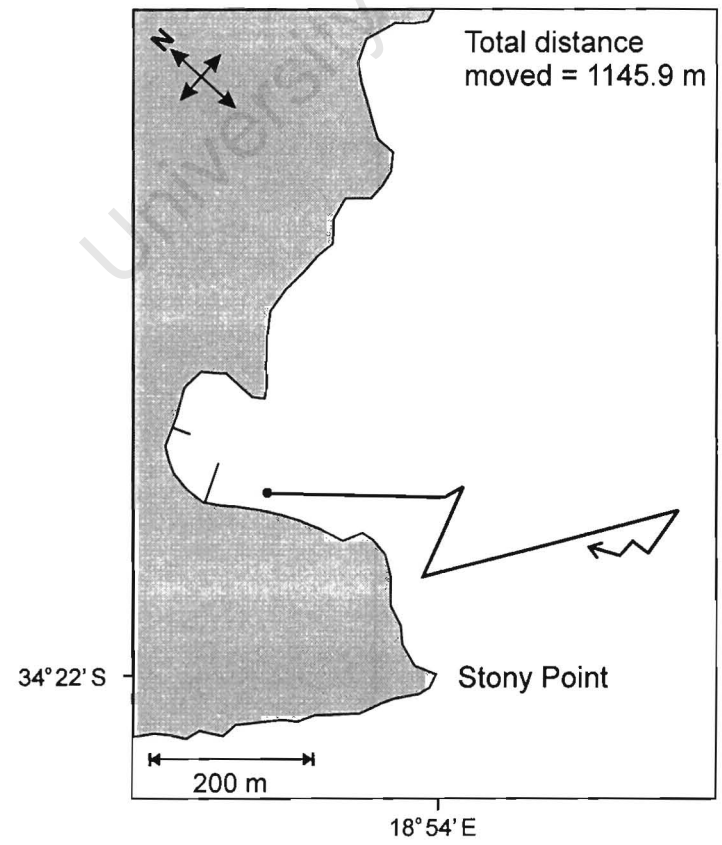

Fig. 6.5: Diagrammatic representation of movements of an acoustically tagged rock lobster (86-mm CL, male), tracked at Betty's Bay on 9 occasions over 32 days.

lobster moved 144 m/day, 212 m/day and 147 m/day, whereas the average rate of movement for the remaining tracking period was 1.6 m/day. The rock lobster covered depths of between 5 m and 15 m during the tracking period, and appeared to be reversing its original route when the transmitter was removed on day 32 (Fig. 6.5).

A frequency distribution of the distance moved in meters per day by all four rock lobsters cumulatively, shows that most movements were between one and five meters per day (Fig. 6.6). On only one occasion did a lobster move less than one meter during a day, and the greatest distance moved was 212 m/day. The average distance moved for all tracked rock lobsters was 15.5 m/day.

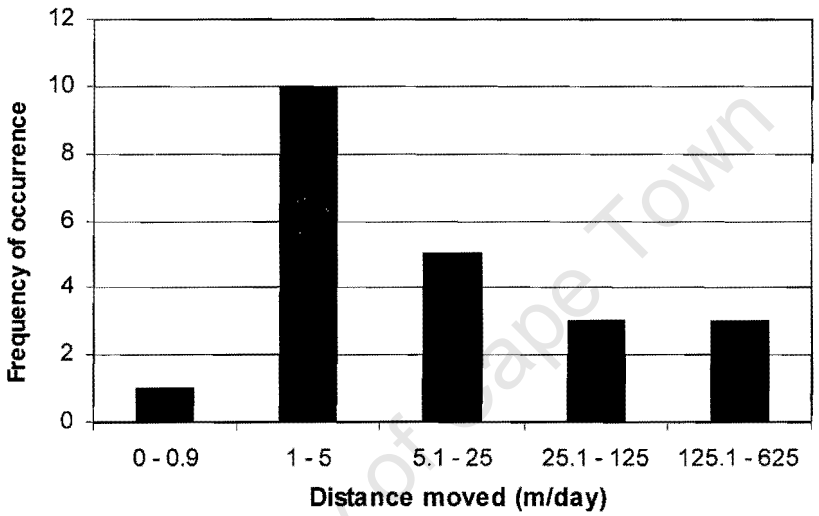

Fig. 6.6: Cumulative frequency of occurrence of the distances moved by four tracked rock lobsters.

6.4 Discussion

The earliest lobster movement studies conducted by means of remote sensing were initiated more than 25 years ago (Chapman *et al.* 1975; Herrnkind *et al.* 1975). Since then, remote sensing has been used to track several commercially important lobster species, such as *Jasus edwardsii* (Kelly 1999), *J. novaehollandiae* (Ramm 1980), *Panulirus cygnus* (Jernakoff *et al.* 1987), *Homarus americanus* (Tremblay *et al.* 1999) and *H. gammarus* (van der Meeren 1997; Smith *et al.* 1998, 2000). However, no studies to date have utilised this approach to track the movements of the West Coast rock lobster, *Jasus lalandii,* despite the fact that it supports the third largest commercial fishery in South Africa. Acoustic telemetry has been identified as the most suitable means of tracking the movements of spiny lobsters (Cote *et al.* 1998). However, initial concerns about applying the technique to track *Jasus lalandii* included the possible negative effects of the transmitter on the movements of the individual (Chapter 5) and the possibility that the signal would be distorted by rocky reefs and dense kelp beds, which are the natural habitat of this species. This study is thus the first to investigate the practicalities of tracking *Jasus lalandii* by acoustic means.

My study was primarily to test the feasibility of using the acoustic transmitters, VEMCO V8-2LR to trace the movement patterns of *J. lalandii.* In this respect, the results were extremely encouraging. The signal could readily be detected from a distance of around 100 m using surface tracking equipment, after which underwater tracking equipment, operated by a diver, allowed precise location and visual inspection of the tagged rock lobster. The signal was easily detected, even when rock lobsters were concealed deep in crevices, indicating that rock does not deflect or seriously attenuate the acoustic signal's passage. The dense kelp beds in which the rock lobsters were tracked, were dominated by the kelp *Ecklonia maxima,* which has a hollow, gas-filled stipe. There were concerns that this feature of the kelp would distort or deflect the acoustic signal but, in reality, they created no problem. On two instances, the acoustic signal was, however, either weakened or not detected at all. The first occasion occurred when a diver placed the transmitter in the sleeve of his wetsuit and swam away from the boat. No signal was detected using either the surface or underwater tracking equipment. On a second occasion, the acoustic signal was notably weakened when the boat turned sharply, causing air bubbles from the engine propellers to surround the hydrophone. These events indicate that air (either from the neoprene in the wetsuit or from the engine propellers) can prevent detection of the acoustic signal. In a similar way, breaking waves close to the shore attenuate the signal (Priede 1992) and acoustic tracking in such environments may be problematic.

There was wide variation in the movement patterns displayed by the four rock lobsters that were tracked. The shortest gross distance moved was 62 m over 15 days and the greatest distance, 1146 m over 32 days. The lengths of time lobsters were tracked varied according to theoretical battery-life or, in one case, loss of the lobster and transmitter. The fastest rate of movement observed was 212 m/day with the average rate of movement for all four rock lobsters tracked being 15.5 m/day. The rock lobster that moved the greatest distance (Fig. 6.5) appeared to be retracing its route back towards the shallows, but at that stage the transmitter had to be removed as the battery-life was due to expire. Tracking over longer time periods would elucidate whether rock lobsters retrace their outward routes. Displacement of rock lobsters and subsequent tracking of their movements would resolve if there is any homing behaviour in this species.

One acoustically tracked rock lobster was known to have moved across a sand-flat area on the first day of tracking (Fig. 6.3) at a rate of 39 m/day. Thereafter the rock lobster remained in the kelp and had an average movement of 7.2 m/day. Although this is an isolated observation, it follows the pattern discribed in Chapter 5, where rock lobsters were detected to move significantly faster in those areas of a tank where there were no shelters, compared to areas with shelters.

To track an individual lobster for a period of time longer than the battery-life allows, would involve replacing the battery. The type of transmitters used in this study had a replaceable battery option. Due to the method used to attach the transmitter, however, the lobster must be removed from the water, the transmitter pried off, a new battery attached and then the transmitter re-attached to the lobster in order to replace the battery. This process could take a lengthy period of time (up to 15 minutes) and would cause considerable disturbance to the rock lobster. Excessive disturbance due to capture and handling is known to induce short-term emigration in rock lobsters (Jernakoff 1987; MacDiarmid *et al.* 1991).

Although the presence of the transmitter on the carapace of the rock lobster was shown not to have any adverse effects on the movement of lobsters (Chapter 5), the possibility exists that capture and handling, associated with the attachment of the transmitter, might have increased initial movement (Herrnkind 1980). MacDiarmid *et al.* (1991) tested the effect of capture on the movements of *Jasus edwardsii* and found there was an increased likelihood of lobsters moving away in the first 24 hours following capture. Jernakoff (1987) suggested that the effects of capture and handling could influence the behaviour of *Panulirus cygnus* for up to a week after

tagging. There are, however, as yet no means of tracking individual rock lobsters without attaching some tracking device. Kelly (1999) used cable ties to attach acoustic transmitters to *J. edwardsii* entirely underwater. The whole process took less than 10 minutes and the lobsters were returned to the same shelter from which they were captured. This method of transmitter attachment minimizes the amount of disturbance, but does increase the bulk of the structure used to attach the transmitter. The same method of transmitter attachment could not be used on *J. lalandii,* however, due to the smaller size of this species. My results do not allow a quantitative evaluation of whether handling altered the initial behaviour of the lobsters, but they do show that the average distances moved in the first 3 – 5 days after release were not obviously greater than those later on.

One tagged rock lobster was lost on day 22 of the intended 32-day tracking period. The loss of this rock lobster may have been due to movement out of the searched area, failure to detect the acoustic signal within the searched area, transmitter failure or the lobster being illegally fished out of the area. The probability that the rock lobster moved out of the searched area, or that the signal was simply not detected, are unlikely. An area in excess of 2 km^2 surrounding the last known position of the lobster was searched thoroughly on three occasions. Considering the average daily rate of movement shown in this study (15.5 m/day), and even the greatest individual movement (212 m/day), it is unlikely that the rock lobster was simply not detected in the area. Transmitter failure after 22 days is unlikely, but cannot be eliminated as a possible explanation. However, I believe, the most likely explanation for the disappearance of the transmitter signal was illegal removal of the rock lobster. Poaching of marine life (particularly *Haliotis midae* and *Jasus lalandii*) is a well-known occurrence along this stretch of coastline (Hauck 1999; Hauck & Sweijd 1999).

The primary focus of this study was to test the utility of the acoustic tracking procedures, specifically for *Jasus lalandii,* and not to apply the methodology to fully explore the movement patterns thereof. Nevertheless, the results, although preliminary, are of interest in themselves and allow at least a qualitative comment on the movement patterns observed.

On only one occasion was a rock lobster observed to move less than 1 m/day. During most tracking observations, the rock lobsters had moved between one and five meters (Fig. 6.6). This further implies that the high shelter-fidelity displayed by rock lobsters in the mesocosmal aquarium studies (Chapter 3) was induced by the intense predatory threat that was present, and is not normal behaviour in the field. During field observations of antennally-tagged rock lobsters,

most lobsters displayed movements of between one and five meters (Chapter 4, Fig. 4.9), similar to the findings of this chapter (Fig. 6.6). The rate and range of movements detected by acoustic tracking supports the findings of Chapter 4. Acoustically tracking rock lobsters showed that *J. lalandii,* on average, move 15.5 m/day, but can move up to 212 m/day, strongly implying that if a home range, does exist for this species, it is considerably larger than the 1250 m^2 surveyed in Chapter 4.

In conclusion, this pilot study successfully demonstrated the effectiveness, accuracy and efficiency of acoustically tracking the movements of *Jasus lalandii* in dense kelp beds, even when sheltering in rocky crevices. Further acoustic studies, with longer tracking periods and to trace the movements of rock lobsters that are experimentally displaced, are logical next steps now that the utility of the methodology has been demonstrated. The implications of accurately determining the range of *Jasus lalandii* movement patterns are considerable. Amongst other things, the knowledge would resolve the extent of movements between fishing grounds, during onshore-offshore seasonal movements and would greatly assist in establishing the effective size of marine reserves required for protection of this species.

Chapter 7

Synthesis

The primary purpose of this thesis was to use a wide range of apparatus and techniques directed at examining different aspects of rock-lobster movement. In doing so, I employed (1) long-term data from tagged, released and recaptured rock lobsters, (2) observations of individual lobsters in a quasi-natural mesocosm aquarium, (3) field monitoring by divers of activity, movements and abundance, (4) observations in small aquaria and (5) acoustic tracking to follow the movements of individual lobsters.

Within the scope of an MSc study, it was not possible to obtain definitive results from all of these different approaches. Rather, the intention was to explore the utility of these techniques for determining rock-lobster movement patterns and to examine their benefits and disadvantages. Like most theses, this study has addressed several hypotheses that were raised, created new questions and provides suggestions, not only for refining the techniques used, but also for future research avenues.

The large-scale movement of *Jasus lalandii* on the West Coast of South Africa was primarily investigated using long-term tag-recapture data, obtained in raw format from Marine and Coastal Management (Chapter 2). These data were used to examine movements in excess of 10 km, of adults > 70 mm CL, focusing also on the direction of movement. The proposed hypothesis was that the decrease in CPUE on the West Coast over the last decade was as a result of a migration around the coast, with rock lobsters settling east of Cape Hangklip, the only area in which there has been an increase in rock-lobster abundance over the last decade. Examination of the long-term tag-recapture data showed that only 0.5 % of recaptured rock lobsters moved more than 10 km, with 0.3 % of them moving south-eastwards and 0.2 % north-westwards. Because such a small percentage of rock lobsters moved from their sites of release, I concluded that there was no evidence of any significant large-scale migration long-shore and that migration could not provide an explanation for the increased density of rock lobsters east of Cape Hangklip.

The small-scale movements of a population of rock lobsters were monitored in a mesocosm aquarium where the natural habitat of the species was closely replicated (Chapter 3). One of the aspects not comparable to the natural environment was the high density of predatory fish within the aquarium. The behaviour of *J. lalandii,* in terms of shelter fidelity, aggregation tendencies

and levels of crepuscular activities as a means of predator avoidance, was monitored. The results of this experiment showed that under intense predation levels, rock lobsters displayed high levels of shelter fidelity, a tendency to aggregate in large cavernous shelters and no evidence of crepuscular activity. Their diet comprised predominantly algae, which were available in or close to shelters. The behaviour of rock lobsters in this experiment could not, however, be assumed to be comparable to that in the field and I believe it was strongly influenced by the intense threat of predation.

In the field, a rock-lobster population east of Cape Hangklip was monitored monthly for changes in abundance, activities and small-scale movement patterns relating to hole and/or site fidelity (Chapter 4). The seasonal abundance, size and sexes of rock lobsters occurring within a marine reserve and a non-reserve area were compared. The rock lobsters displayed no fidelity to specific holes. If any site fidelity existed, it was over an area in excess of 1250 m^2 the size of the area monitored, but the conservative conclusion is that *J. lalandii* does not display site fidelity. A seasonal onshore-offshore movement was evident at the reserve and non-reserve sites with ovigerous female rock lobsters being found in higher abundance inshore during the winter months, gradually switching to a higher abundance of males towards the onset of summer. Large rock lobsters (> 80 mm CL) were in higher abundance at the reserve site compared to the non-reserve site during both open and closed recreational fishing seasons. The diet of rock lobsters in this area comprised largely algae, reaffirming the hypothesis that there is low abundance of more normal prey items in this area.

The effects of acoustic transmitters on the movements of *J. lalandii* over 85 mm CL, were tested in a laboratory. Simultaneously the behaviour of lobsters near to *vs.* far from shelters was monitored, in the absence of predators (Chapter 5). The transmitters had no adverse effects on the movement rates or feeding of rock lobsters. Lobsters remained near shelters unless food was made available, in which case they moved rapidly towards the food, foraged or secured a piece of food and then moved back to the shelters. Even in the absence of predators, the rock lobsters had a faster rate of movement when they were away from shelters than when they were in their vicinity.

An acoustic tracking pilot study successfully demonstrated the feasibility of using this technique to monitor the movements of *J. lalandii* in its natural environment. Although this study was based on a small sample size, the results, nevertheless, yield a movement rate of 15.5 m/day and a maximum distance moved of 1146 m over 32 days. The mean rate of movement implies that if

J. lalandii has a home range, it will almost certainly be larger than the 1250 m^2 surveyed in Chapter 4. The rapid rates of movement over short periods of time displayed by rock lobsters in this study have considerable implications for the management of the species, particularly in terms of the role of rock-lobster sanctuaries and marine protected areas.

Obtaining thorough information on palinurid movements is difficult and expensive (Herrnkind 1980). The species are widely distributed, the environment is foreign to the researcher and inferring natural patterns from confined studies is frequently imprecise. However, by applying an integrated approach and using a range of techniques, the negative aspects of one method may be balanced by another's positive ones. Each technique used to monitor the movement patterns of *J. lalandii* in this study also has advantages and disadvantages. Table 7.1 summarizes aspects of each monitoring technique used.

Table 7.1: A summary of aspects of the five methods used to examine the movements of rock lobsters in this study.

	Commercial tag-recapture		Mesoscale aquarium		Small-scale aquaria		Field observations by divers		Acoustic tracking	
Control over environment	nil	X	partial	√	substantial	√	nil	X	nil	X
Sample size	large	√	medium	√	medium	√	medium	√	small	X
Accuracy of movement recorded	poor	X	limited	X	good	√	limited	X	good	√
Replication	annual	√	none	X	good	√	limited	√	limited	√
Practicality	good	√	moderate	√	good	√	poor	X	good	√
Area covered	large	√	small	X	very small	X	moderate	√	large	√
Temporal coverage	multiple years	√	months	√	months	√	months	√	weeks	X
Approximation to nature	natural	√	quasi-natural	X	artificial	X	natural	√	natural	√

Large-scale tag-recapture programs, often associated with the commercial fishery, allow wide geographic coverage and establishment of a long-term database. Large amounts of data are collected at low expense for the researcher. The data obtained in this manner are, however, often biased by fishing occurring only in areas known to support lucrative rock-lobster catches, but an absence of fishing, and hence no sampling, in areas that are not favoured. The greatest proportion of recaptures will occur where the fishing effort is greatest, even if lobsters disperse randomly. This sampling procedure may thus suggest a movement trend that does not exist in reality.

With large-scale field observations such as this, no control over environmental conditions and temporal or spatial differences in conditions can only be factored in if extensive monitoring takes place. Experimental manipulations are not possible. Conversely, conditions are natural, - at least as natural as they can be in harvested systems.

Monitoring the movements of rock lobsters in a mesoscale environment provides the opportunity to observe an entire, introduced population under controlled conditions. However, in my study, the mesoscale environment, although closely resembling the natural habitat of rock lobsters, had the primary function of being a display tank and conditions therein could not be controlled or varied as I might have wished. In particular the densities of predators were unnaturally high. For this reason, the movements of rock lobsters were considered to be substantially influenced by the intense predation levels. An important limitation was the impossibility of spatial replication or manipulation of predator densities.

I also used small-scale laboratory aquaria in some of my experiments. They have the advantage of replication and control over conditions. Paradoxically, these very benefits make it problematic to extrapolate the results to field conditions.

Visually monitoring rock lobsters over time by means of divers allows direct observations of densities, habitat and behaviour. The amount of data collected is limited by the size of the area divers are able to effectively search. Although replicate data can be collected, providing an indication of possible movements into or out of the area, the knowledge gained is restricted to the areas searched. Sampling can be negatively influenced by poor weather conditions, leading to misinterpretation of data and incorrect conclusions. Areas that differ can be compared as, for example, was done in this study, comparing a harvested and a protected area. Confidant extrapolation of such comparisons depends on replication of sites, and my comparison was inadequate in this respect.

Tracking rock lobsters using acoustic techniques allows definitive monitoring of the rate, direction and time of movement. Each lobster can individually be followed over large distances and easily tracked even when sheltering under rock or in dense kelp. Provided the transmitter remains attached to the lobster and can be detected using the receiver, the data are relatively precise and can be collected in real time. Bad weather conditions can hamper tracking, limiting the range of transmitter detection. There is also a limited number of tracking frequencies available, restricting the number of individuals that can be tracked at one time.

The approach (or combination of approaches) that is most appropriate for monitoring rock-lobster movement depends largely on the precise question that is being asked. By integrating the various approaches, I could begin to decipher the movement patterns of *J. lalandii* at various scales. Some of the results yielded conclusions that are robust and likely to be definitive. I am, for instance, certain that large-scale long-shore movements of adult lobsters do not take place. Other results are more vague. The mesocosm aquarium observations suggest that, because the threat of predation was high, lobsters displayed extreme fidelity to holes and seldom left their shelters. The generality of this conclusion could not be tested because of the impossibility of replicating or manipulating circumstances. When I explored hole fidelity in the field, it seemed non-existent. This example illustrates the difficulties of generalizing from laboratory findings to field conditions, particularly when constraints are placed on replication and manipulation.

A seasonal study of rock-lobster abundance in the field suggests that some degree of inshore-offshore movement occurs at different times of the year for males and females. This data collection was, however, not replicated and is only applicable for the year in which monitoring took place. Further studies are necessary to confirm regular occurrence of these movement patterns.

I am confidant that my small-scale aquarium experiments reasonably demonstrate that acoustic transmitters did not influence the movement-capabilities of lobsters, because the work was adequately replicated and comparisons were made with control animals. The observations on rate of movement, when lobsters are near to or far from shelters, are strongly suggestive of risk-avoidance, but their validity could be more rigorously tested by altering predator threat and with further field based observations.

The most promising technique used to monitor the movements of *J. lalandii* in this study was acoustic tracking. It is strongly recommended that further studies be conducted using this technique, including: (1) lengthening the tracking period by replacing the transmitter battery as efficiently as possible, and returning the lobster to the same hole in which it was found, thus minimizing disturbance; (2) tracking experimentally displaced rock lobsters to test their homing ability and provide an indication of whether home-ranges exist and, if so, the home-range size (3) tracking both males and females, especially during the seasonal period when inshore–offshore movements are most likely, as suggested in Chapter 4; (4) increasing the number of individuals tracked at one time to a maximum of ten (dictated by the number of frequencies

available and time taken for tracking per day) and (5) acoustic tracking should be used to monitor the movement of individuals prior to and during anoxia events and to track rock lobsters returned to different areas after a red tide.

A further recommendation would be to continue monitoring the commercial tag-return data for large-scale movements, but to also tag females and rock lobsters of both sexes in the smaller size classes. This would investigate the possibility of juvenile *J. lalandii* migrating long-shore to counteract larval displacement by prevailing currents, which currently cannot be examined using this technique because only adults are tagged.

Finally, I would also recommend the continuation of seasonal, quarterly diver-surveys at inshore bays in the area east of Cape Hangklip to determine patterns of rock-lobster size and sex abundance inshore. The substantial increases of density in this area in the past decade has dramatically transformed the ecosystem, and ongoing studies on the movements and population dynamics of lobsters there remains of intense interest.

Literature cited

Anderka, F. W. and Angerhrn, P. (1992). Transmittor attachment methods. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals.* (ed. I. G. Priede and S. M. Swift), pp 670. Great Britain: Ellis Horwood Ltd.

Annala, J. H. (1981). Movements of rock lobsters (*Jasus edwardsii*) tagged near Gisborne, New Zealand. *New Zealand Journal of Marine and Freshwater Research.* 15, 437-443.

Annala, J. H. and Bycroft, B. L. (1993). Movements of rock lobsters (*Jasus edwardsii*) tagged in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27, 183-190.

Attwood, C. G. and Bennett, B. A. (1994). Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Canadian Journal of Fisheries and Aquatic Science* 51, 1247-1257.

Babcock, R. C., Kelly, S., Shears, N. T., Walker, J. W. and Willis, T. J. (1999). Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* 189, 125-134.

Barkai, A., Davis, C. L. and Tugwell, S. (1996). Prey selection by the South African Cape rock lobster *Jasus lalandii*: Ecological and physiological approaches. *Bulletin of Marine Science* 58, 1-8.

Barshaw, D. E. and Able, K. W. (1990). Tethering as a technique for assessing predation rates in different habitats: An evaluation using juvenile lobsters *Homarus americanus. Fishery Bulletin* 88, 415-417.

Bennett, B. A. and Attwood, C. G. (1991). Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Marine Ecology Progress Series* 75, 173-181.

Beyers, C. J. D. B., Wilke, C. G. and Goosen, P. C. (1994). The effects of oxygen deficiency on growth, intermoult period, mortality and ingestion rates of aquarium-held juvenile rock lobster *Jasus lalandii*. *South African Journal of Marine Science* 14, 79-87.

Booth, J. D. (1984). Movements of packhorse rock lobsters (*Jasus verreauxi*) tagged along the eastern coast of the North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 18, 275-281.

Booth, J. D. (1997). Long-distance movements in *Jasus* spp. and their role in larval recruitment. *Bulletin of Marine Science* 61, 111-128.

Booth, J. D. and Ovenden, J. R. (2000). Distribution of *Jasus* spp. (Decapoda: Palinuridae) phyllosomas in southern waters: implications for larval recruitment. *Marine Ecology Progress Series* 200, 241-255.

Caccamise, D. F. and Hedin, R. S. (1985). An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 97, 306-318.

Campbell, A. (1986). Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. *Canadian Journal of Fish and Aquatic Science* 43, 2197-2205.

Campbell, A. and Stasko, A. B. (1986). Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Marine Biology* 92, 393-404.

Caputi, N., Fletcher, W. J., Pearce, A. and Chubb, C. F. (1996). Effect of the Leeuwin current on the recruitment of fish and invertebrates along the western Australian coast. *Marine and Freshwater Research* 47, 147-155.

Chapman, C. J., Johnstone, A. D. F. and Rice, A. L. (1975). The behaviour and ecology of the Norway lobster, *Nephrops norvegicus* (L.). *Proceedings of the 9th European Marine Biology Symposium*, 59-74.

Childress, M. J. (1997). Marine Reserves and their effects on lobster populations: Report from a workshop. *Marine and Freshwater Research* 48, 1111-1114.

Cobb, J. S. (1997). Oceanic processes affecting lobster larvae: Report from a workshop. *Marine and Freshwater Research* 48, 771-775.

Cockcroft, A. C. and Goosen, P. C. (1995). Shrinkage at moulting in the rock lobster *Jasus lalandii* and associated changes in reproductive parameters. *South African Journal of Marine Science* 16, 195-203.

Cockcroft, A. C., Schoeman, D. S., Pitcher, G. C., Bailey, G. W. and Van Zyl, D. L. (1998). A mass stranding, or 'walk out' of West Coast rock lobster, *Jasus lalandii*, in Elands Bay, South Africa: Causes, results and implications. In *Fourth International Crustacean Congress*, vol. 11 (ed. J. Carel Von Vaupel Klein and J. R. Schram), pp. 673-688. Amsterdam, The Netherlands: A. A. Balkema Publishers.

Collins, K. J. and Jensen, A. C. (1992). Acoustic tagging of lobsters on the Poole Bay artificial reef. In *Wildlife Telemetry - Remote Monitoring and Tracking of Animals* (ed. I. G. Priede and S. M. Swift). New York: Ellis Horwood Ltd.

Cote, D., Scruton, D. A., Niazgoda, G. H., McKinlay, R. S., Rowsell, D. F., Lindstrom, R. T., Ollerhead, L. M. N. and Whitt, C. J. (1998). A coded acoustic telemetry system for high precision monitoring of fish location and movement: Application to the study of nearshore nursery habitat of juvenile Atlantic cod (*Gadus Morhua*). *Marine Technological Society Journal* 32 (1), 54-62.

Day, E. and Branch, G. M. (2000a). Evidence for a positive relationship between juvenile abalone *Haliotis midae* and the sea urchin *Parechinus angulosus* in the South-Western Cape, South Africa. *South African Journal of Marine Science* 22, 145-156.

Day, E. and Branch, G. M. (2000b). Relationships between recruits of abalone *Haliotis midae*, encrusting corallines and the sea urchin *Parechinus angulosus*. *South African Journal of Marine Science* 22, 137-144.

Day, E and Branch, G. M. (in press). Direct and indirect effects of the sea urchin *Parechinus angulosus* on recruits and juveniles of the South African abalone *Haliotis midae*. *Ecology.*

Edgar, G. J. and Barrett, N. S. (1999). Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* 242, 107-144.

Eggleston, D. B. and Lipcius, R. N. (1992). Shelter selection by spiny lobster under variable predation risk, social conditions and shelter size. *Ecology* 73, 992-1011.

Ennis, G. P. (1984a). Small-scale seasonal movement of the American lobster, *Homarus americanus*. *Transactions of the American Fisheries Society* 113, 336-338.

Ennis, G. P. (1984b). Territorial behaviour of the American lobster, *Homarus americanus*. *Transactions of the American Fisheries Society* 113, 330-335.

Estrella, B. T. and Morrissey, T. D. (1997). Seasonal movement of offshore American lobster, *Homarus americanus*, tagged along the eastern shore of Cape Cod, Massachusetts. *Fishery Bulletin* 95, 466-476.

Field, J. G., Griffiths, C. L., Jarman, N., Zoutendyk, P., Velimirov, B. and Bowes, A. (1980). Variation in structure and biomass of kelp communities along the South-Western Cape coast. *Transactions of the Royal Society of South Africa.* 44, 145-203.

Fowler, J. and Cohen, L. (1995). Statistics for Ornithologists. *2nd Edition*: BTO Guide 22. pp.150.

Goosen, P. C. and Cockcroft, A. C. (1995). Mean annual growth increments for male West Coast rock lobster *Jasus lalandii*, 1969 - 1993. *South African Journal of Marine Science* 16, 377-386.

Griffiths, M. H. (2000). Long-term trends in catch and effort of commercial linefish off South Africa's Cape province: Snapshots of the 20th Century. *South African Journal of Marine Science* 22, 81–110.

Grobler, C. A. F. and Noli-Peard, K. R. (1997). *Jasus lalandii* fishery in post-independence Namibia: Monitoring population trends and stock recovery in relation to a variable environment. *Marine and Freshwater Research* 48, 1015-1022.

Groeneveld, J. C. (in press). Long-distance migration of the rock lobster *Palinurus delagoae* off South Africa and Mozambique. *South African Journal of Marine Science* .

Groeneveld, J. C. and Branch, G. M. (in press). Long-distance migration of the rock lobster *Palinurus gilchristi* off South Africa, with implications for juvenile recruitment. *Marine Ecology Progress Series.* .

Haakonsen, H. O. and Anoruo, A. O. (1994). Tagging and migration of the American lobster *Homarus americanus*. *Reviews in Fisheries Science* 2, 79-93.

Hauck, M. (1999). Regulating marine resources in South Africa: The case of the abalone fishery. In *Environmental Justice and the Legal Process* (ed. J. Glazewski and G. Bradfield), pp. 211-228: Juta, Cape Town.

Hauck, M. and Sweijd, N. A. (1999). A case study of abalone poaching in South Africa and its impact on fisheries management. *ICES Journal of Marine Science* 56, 1024-1032.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* 31, 295-311.

Herrnkind, W. (1969). Queuing behaviour of spiny lobsters. *Science* 164, 1425-1427.

Herrnkind, W. F., Van der Walker, J. A. and Barr, L. (1975). Population dynamics, ecology and behaviour of spiny lobsters, *Panulirus argus*, of St. John, U.S. Virgin Islands: Habitation, patterns of movement and general behaviour. *Results of the Tektite Program, Bulletin of the Natural History Museum of Los Angeles County.* 20, 31-45.

Herrnkind, W. F. (1980). Spiny lobsters: Patterns of movement. In *Biology and Management of Lobsters*, Volume 1 (ed. J. S. Cobb and B. F. Phillips), pp. 349-407: Academic Press Inc.

Heydorn, A. E. F. (1969). The rock lobster of the South African West Coast *Jasus lalandii* (H. Milne-Edwards) 2. Populations studies, behaviour, reproduction, moulting, growth and migration. *Division of Sea Fisheries Investigational Report* 71, 1-51.

Hyslop, E. J. (1980). Stomach contents analysis - a review of methods and their application. *Journal of Fisheries Biology* 17, 411-429.

Jernakoff, P. (1987). Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology* 113, 125-144.

Jernakoff, P., Phillips, B. F. and Maller, R. A. (1987). A quantitative study of nocturnal foraging distances of the western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology* 113, 9-21.

Jernakoff, P. and Phillips, B. F. (1988). Effect of a baited trap on the foraging movements of juvenile western rock lobsters, *Panulirus cygnus* George. *Australian Journal of Marine and Freshwater Research* 39, 185-192.

Johnston, S. J. and Bergh, M. O. (1993). Size-based estimates of survivorship for the South African rock lobster *Jasus lalandii*. *Fisheries Research* 18, 277-304.

Karnofsky, E. B., Atema, J. and Elgin, R. H. (1989). Field observations of social behaviour, shelter use and foraging in the lobster, *Homarus americanus*. *Biological Bulletin* 176, 239-246.

Kelly, S. (1999). Marine reserves and the spiny lobster, PhD thesis, pp. 145. University of Auckland, New Zealand.

Kelly, S., Scott, D., MacDiarmid, A. B. and Babcock, R. C. (2000). Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* 92, 359-369.

Koike, T., Maegawa, M. and Nagata, Y. (1997). Automatic recording systems for lobster movements in an experimental tank. *Bulletin of Marine Science* 61, 139-146.

Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68, 619-640.

Lipcius, R. N. and Herrnkind, W. F. (1985). Photoperiodic regulation and daily timing of spiny lobster mating behaviour. *Journal of Experimental Marine Biology and Ecology* 89, 191-204.

Lozano-Alvarez, E. and Spanier, E. (1997). Behaviour and growth of captive spiny lobsters (*Panulirus argus*) under the risk of predation. *Marine and Freshwater Research* 48, 707-713.

Lutjeharms, J. R. E. and Ballegooyen, R. C. V. (1988). Anomalous upstream retroflection in the Agulhas current. *Science* 240, 1770-1772.

MacDiarmid, A. B. (1991). Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster *Jasus edwardsii* on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* 70, 129-141.

MacDiarmid, A. B., Hickey, B. and Maller, R. A. (1991). Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* 147, 185-205.

MacDiarmid, A. B. and Breen, P. A. (1992). Spiny lobster population change in a marine reserve. In *Proceedings of the Second International Temperate Reef Symposium* (ed. C. N. Battershill, Schiel D. R., Jones G. P., Creese R. G., MacDiarmid A. B.), pp. 47-56 / 252 p. Auckland, New Zealand.

Matthews, S. G. and Pitcher, G. C. (1996). Worst recorded marine mortality on the South African coast. In *Harmful and Toxic Algal Blooms* (ed. T. Yasumoto, Oshima, Y and Fukuyo, Y.), pp. 89-92.

Mayfield, S., and Branch, G. M. (2000). Interrelations among rock lobsters, sea urchins, and juvenile abalone: Implications for community management. *Canadian Journal of Fish and Aquatic Sciences* 57, 2175-2185.

Mayfield, S., Atkinson, L. J., Branch, G. M. and Cockcroft, A. C. (2000a). Diet of the West Coast rock lobster *Jasus lalandii*: Influence of lobster size, sex, capture depth, latitude and moult stage. *South African Journal of Marine Science* 22, 57-69.

Mayfield, S., Branch, G. M. and Cockcroft, A. C. (2000b). Relationships among diet, growth rate and food availability for the South African rock lobster *Jasus lalandii* (Decapoda, Palinuridae). *Crustaceana* 73, 815-834.

Mayfield, S., Branch, G. M. and Cockcroft, A. C. (in press). The effects of Marine Protected Areas on the fishery for the South African rock lobster, *Jasus lalandii*. *Marine and Freshwater Research.*

McKoy, J. L. (1983). Movements of rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae), tagged near Stewart Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 17, 357-366.

Meeren, G. I. v. d. (1997). Preliminary acoustic tracking of native and transplanted European lobsters (*Homarus gammarus*) in an open sea lagoon. *Marine and Freshwater Research* 48, 915-921.

Meyer-Rochow, V. B. (1994). Light-induced damage to photoreceptors of spiny lobsters and other crustaceans. *Crustaceana* 67, 95-109.

Milton, R. (1953). Sea Plant Feeds. Portland Place: Analytical and Consulting Chemist.

Montgomery, S. S. and Brett, P. A. (1996). Tagging eastern rock lobsters *Jasus verreauxi*: effectiveness of several types of tag. *Fisheries Research* 27, 141-152.

Moore, R. and MacFarlane, J. W. (1984). Migration of the ornate rock lobster (*Panulirus ornatus* Fabricus), in Papua New Guinea. *Australian Journal of Marine and Freshwater Research* 35, 197-212.

Moriyasu, M., Landsburg, W. and Conan, G. Y. (1993). Sphyrion tag shedding and tag induced mortality of the American lobster, *Homarus americanus* H. Milne-Edwards, 1837 (Decapoda, Nephropidae). *Crustaceana* 68, 184-192.

Newland, P. L. and Chapman, C. J. (1993). Locomotory behaviour and swimming performance of the Norway lobster, *Nephrops norvegicus*, in the presence of an acoustic tag. *Marine Biology* 115, 33-37.

Newman, G. G. and Pollock, D. E. (1971). Biology and migration of rock lobster *Jasus lalandii* and their effect on availability at Elands Bay, South Africa. *Division of Sea Fisheries Investigational Report* 94, 1-24.

Newman, G. G. and Pollock, D. E. (1974). Biological cycles, maturity and availability of rock lobster *Jasus lalandii* on two South African fishing grounds. *Division of Sea Fisheries Investigational Report.* 107, 1-16.

Noli, K. R. and Grobler, C. A. F. (1998). Seasonal migration of Namibian rock lobster. *Namibia Brief* 20, 126-128.

O'Dor, R. K. and Webber, D. M. (1991). Ultrasonic telemetry. In *The Lobster Newsletter*, vol. 4, pp. 1-2.

O'Dor, R. K., Andrade, Y., Webber, D. M., Sauer, W. H. H., Roberts, M. J., Smale, M. J. and Voegeli, F. M. (1998). Applications and performance of Radio-Acoustic Positioning and Telemetry (RAPT) systems. *Hydrobiologia* 371/372, 1-8.

Paterson, N. F. (1969). The behaviour of captive Cape rock lobsters, *Jasus lalandii* (H. Milne-Edwards). *Annals of the South African Museum* 52, 225-264.

Phillips, B. F. and Pearce, A. F. (1997). Spiny lobster recruitment off Western Australia. *Bulletin of Marine Science* 61, 21-41.

Pitcher, G. C. (1998). Harmful algal blooms of the Benguela current, pp. 20. Cape Town: National Book Printers.

Pitcher, G. C. and Calder, D. (2000). Harmful algal blooms of the southern Benguela current: A review and appraisal of monitoring from 1989 to 1997. *South African Journal of Marine Science* 22, 255-271.

Pollock, D. E. (1982). The fishery for and population dynamics of West Coast rock lobster related to the environment in the Lamberts Bay and Port Nolloth areas. *Division of Sea Fisheries Investigational Report* 124, 1-53.

Pollock, D. E. (1991). Justification for West Coast rock lobster sanctuaries. Sea Fisheries Research Institute, Cape Town. West Coast rock lobster working group report number WG/06/91/WCL1, pp. 15.

Pollock, D. E. (1994). The fisheries for two *Jasus* species of the South-East Atlantic and for *Palinurus gilchristi* off the southern Cape Coast of South Africa. In *Spiny Lobster Management* (ed. B. F. Phillips, J. S. Cobb and J. Kittaka). Great Britain: Blackwell Scientific Publications.

Pollock, D. E. and Shannon, L. V. (1987). Response of rock lobster populations in the Benguela ecosystem to environmental change - a hypothesis. *South African Journal of Marine Science* 5, 887-899.

Pollock, D. E., Cockroft, A. C. and Goosen, P. C. (1997). A note on reduced rock lobster growth rates and related environmental anomalies in the southern Benguela, 1988-1995. *South African Journal of Marine Science* 18, 287-293.

Priede, I. G. (1992). Wildlife Telemetry: An Introduction. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals.* (ed. I. G. Priede and S. M. Swift), pp 670. Great Britain: Ellis Horwood Ltd.

Ramm, D. C. (1980). Electromagnetic tracking of rock lobsters (*Jasus novaehollandiae*). *Australian Journal of Marine and Freshwater Research.* 31, 263-269.

Roberts, C. (in press). Benefits of no-take marine reserves for migratory species. *Reviews in Fish Biology and Fisheries.*

Saila, S. B. and Flowers, J. M. (1968). Movements and behaviour of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. *Journal du Conseil, conseil permanent international pour L' Exploration du la Mer.* 31, 342-352.

Scarrat, D. J. and Elson, P. F. (1965). Preliminary trials of a tag for salmon and lobsters. *Journal of Fisheries Research Board of Canada.* 22, 421-423.

Silberbauer, B. I. (1971). The biology of the South African rock lobster, *Jasus lalandii* (H. Milne edwards). *Division of Sea Fisheries Investigational Report* 92, 1-70.

Smith, I. P., Collins, K. J. and Jensen, A. C. (1998). Movement and activity patterns of the European lobster, *Homarus gammarus*, revealed by electromagnetic telemetry. *Marine Biology* 132, 611-623.

Smith, I. P., Collins, K. J. and Jensen, A. C. (2000). Digital electromagnetic telemetry system for studying behaviour of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 247, 209-222.

Spanier, E. (1994). What are the characteristics of a good artificial reef for lobsters? *Crustaceana* 67, 173-186.

Spanier, E. and Zimmer-Faust, R. K. (1988). Some physical properties of shelter that influence den preference in spiny lobsters. *Journal of Experimental Marine Biology and Ecology* 121, 137-149.

Spanier, E., McKenzie, T. P., Cobb, J. S. and Clancy, M. (1998). Behaviour of juvenile American lobsters, *Homarus americanus*, under predation risk. *Marine Biology* 130, 397-406.

Stasko, A. B. and Pincock, D. G. (1977). Review of underwater biotelemetry, with emphasis on ultrasonic techniques. *Journal of the Fisheries Research Board of Canada.* 34, 1261-1285.

StatSoft, Inc. (1995). STATISTICA for Windows (Computer program manual). Tulsa, OK: StatSoft, Inc., 2300 East 14th Street, Tulsa, OK.

Tarr, R. J. Q., Williams, P. V. G. and MacKenzie, A. J. (1996). Abalone, sea urchins and rock lobster: A possible ecological shift that may affect traditional fisheries. *South African Journal of Marine Science* 17, 319-323.

Tomalin, J. B. (1993). Migrations of spiny rock lobster, *Jasus lalandii*, at Lüderitz: Environmental causes and effects on the fishery and benthic ecology. MSc thesis. pp. 99. University of Cape Town, South Africa.

Tremblay, M. J., Duggan, R., O'Dor, R., Curtis, C., Webber, D. and Andrade, Y. (1999). Daily movements of lobsters from ultrasonic tracking. *Journal of Shellfish Research* 18, 307.

Vannini, M. and Cannicci, S. (1995). Homing behaviour and possible cognitive maps in crustacean decapods. *Journal of Experimental Marine Biology and Ecology* 193, 67-91.

Waddy, S. L. and Aiken, D. E. (1992). Seasonal variation in spawning by preovigerous American lobster (*Homarus americanus*) in response to temperature and photoperiod manipulation. *Canadian Journal of Fish and Aquatic Science* 49, 114-117.

Williams, M. J. (1981). Method for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology* 52, 103-113.

Wolcott, T. G. and Hines, A. H. (1990). Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). *Bulletin of Marine Science* 46, 83-94.

Zar, J. H. 1984. *Biostatistical Analysis*, 2nd edition. pp. 718. Prentice-Hall, New Jersey.

Zimmer-Faust, R. K. and Spanier, E. (1987). Gregariousness and sociality in spiny lobsters: Implications for den habitation. *Journal of Experimental Marine Biology and Ecology* 105, 57-71.

Zoutendyk, P. (1988). Feeding, defaecation and absorption efficiency in the Cape rock lobster *Jasus lalandii*. *South African Journal of Marine Science* 6, 59-65.